The Sense of Agency:
Neural and Cognitive Correlates of the Self in Action

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1 General Introduction

1.1 What is the sense of agency?

The sense of agency refers to the human ability to perceive causality, in particular, causality between the mind and the body or between the body and the external world (Gallagher, 2000). More specifically, the sense of agency is a person's feeling that he or she can cause and control his or her own actions and produce, through them, changes in the external world.

1.1.1 The problem of perceiving causality

In our daily life it seems natural to us that we are the ones causing the motion of our body when we walk or when we grasp an apple. We also know, without thinking about it, that our actions produce specific effects, for example, that a light turns on when we press the light switch or that certain sounds occur when we utter our name or when we close a door. We have the experience of a coherent link from our thoughts, to our body movements, to the external effects in the world, which brings about a feeling of control of these events.

However, in fact, we are unable to consciously track the causal chain between our conscious will and the resulting bodily or external effects since we are not aware of many aspects of our mental or physical actions (e.g., Fourneret & Jeannerod, 1998; Libet, 1985). As David Hume 1748 already noted, "*The motion of our body follows upon the command of our will. Of this we are every moment conscious. But the means, by which this is effected; the energy, by which the will performs so extraordinary an operation; of this we are so far from being immediately conscious, that it must for ever escape our most diligent enquiry*" (Hume, 1748; 2007, p.47). In the light of this skeptical view of causation, the fundamental question arises that if we cannot possess knowledge about causal processes, then how can we experience causality, and specifically, how does the capacity emerge for experiencing ourselves as causal agents. For instance, what makes us feel that we can control the movement of our eyes or legs better than the contraction of our heart or the size of our pupil? How do we know that a light turning on somewhere in a room was in fact related to our button push on the wall? Why do some patients with schizophrenia have the experience that their own actions are controlled by external forces?

During the last decade the sense of agency has become an increasingly prominent interdisciplinary research topic (for reviews, see Balconi, 2010; David, Newen, & Vogeley, 2008) in the field of psychology (e.g., Aarts, Custers, & Wegner, 2005; Sato & Yasuda, 2005), philosophy (e.g., de Vignemont & Fourneret, 2004; Gallagher, 2000; Pacherie, 2008; Synofzik, Vosgerau, & Newen, 2008a), neuroscience (e.g., Blakemore, Wolpert, & Frith, 1998; Chaminade & Decety, 2002; Farrer et al., 2003), psychiatry (e.g., Daprati et al., 1997; Frith, Blakemore, & Wolpert, 2000b; Heinks-Maldonado et al., 2007) and neurology (e.g., Farrer, Franck, Paillard, & Jeannerod, 2003; Moore et al., 2010). Nevertheless, a thorough understanding of this cognitive function is still lacking because the diversity of conceptualizations, paradigms and measures of agency is huge. It is this very diversity which makes the development of a comprehensive account more difficult.

The present research aims at elucidating some processes behind the experience of agency by combining behavioral and neural measures and by targeting different underlying cognitive operations. The complex phenomenology of the sense of agency suggests that it is not based on a single cortical source but evolves out of the combination of multiple cues and a distributed network of processing modules. Furthermore, a case of a possible disturbance of agency as it is apparent in the phenomenology of obsessive-compulsive disorder will be considered in order to study a selective breakdown and work out the details of the agency system.

1.1.2 Feeling versus judging: the phenomenology of agency

When we talk about a sense of agency, that is, the perception of self-causality we are not referring to a single, circumscribed experience but to a category composed of distinct, separable experiential dimensions. In particular, two dimensions have been distinguished, the feeling and judgment of agency (Synofzik, Vosgerau, & Newen, 2008a, 2008b).

The feeling of agency represents a non-conceptual experience of self-causality. It is present as a diffuse background feeling of coherent sensory-motor and motor-sensory flow. A sound, for example, is perceived as being coupled to one's action in an implicit way, without consciously reflecting about it. That is, the feeling of agency is not based on a conscious decision about what might be the most plausible cause of a sound, but an event is merely automatically classified as being caused by one's action or not. A disturbance at this level may show up in feelings of incompleteness or doubts about actions. For example, a person may have the sensation when locking a door that the door is not locked just right or when talking to people that the words do not sound just right, as observed in patients with obsessive-compulsive disorder (Coles, Frost, Heimberg, & Rheaume, 2003).

The judgment of agency, in contrast, is a conceptual, attributive explanation of self-causality: the potential causes of a sensory event such as a sound are taken into account and a belief is formed about the origins of that sound and the degree of personal influence. A disturbance at this level of belief formation may be reflected in auditory hallucinations of patients with schizophrenia (Heinks-Maldonado et al., 2007), in delusional beliefs that one's body is controlled by an external agent (Bell, Halligan, & Ellis, 2006; Synofzik, Vosgerau, & Newen, 2008a) or in anarchic limb phenomena and anosognosia for hemiparesis (Synofzik, Vosgerau, & Newen, 2008b).

In our everyday life, the feeling of agency is more prevalent than the judgment of agency: when we act a feeling of motor-sensory flow is constantly present and only in cases of discrepancy or in unfamiliar contexts (e.g., during the acquisition of new skills) we consciously monitor and judge our causal influence. Current research on the sense of agency, however, does not do justice to this fact but, to the contrary, so far mostly explicit measures are used which capture the judgment level of agency only (see also chapter 1.3.1). In the present work, both the feeling and judgment of agency are investigated empirically, and the umbrella term sense of agency (or agency experience) is used to subsume both experiential dimensions.

1.1.3 Construing a sense of self

The sense of agency is considered an essential feature of self-consciousness, in particular, it refers to the awareness of the results of the self in action (Georgieff & Jeannerod, 1998; Knoblich, Elsner, Aschersleben, & Metzinger, 2003). What has been recognized for experiences and thoughts is also true for actions in that they do "…not just occur in a free-floating way, like clouds in the sky, but seem to originate from—and within—a thinking self, a self somehow mentally portrayed as an independent cause in itself, a cognitive agent" (Knoblich, Elsner, Aschersleben, & Metzinger, 2003, p.487).

An important distinction has been drawn between two variants of self-consciousness: First, the “minimal self” (Gallagher, 2000; or "physical self", Gillihan & Farah, 2005; or "embodied self", Jeannerod, 2007) refers to the (non-conscious) awareness of one’s own body or action during a particular bodily event. It is thought to be composed of the feeling of agency along with the sense of ownership for body parts (Gallagher, 2000; Tsakiris, Schütz-Bosbach, & Gallagher, 2007). A second variety of the self is the “narrative self” (Gallagher, 2000; or "psychological self", Gillihan & Farah, 2005) involving autobiographical memory and beliefs about one’s traits and attitudes which continue and develop across time and experiences. The judgment of agency may be considered a source for the “narrative self”, in particular, for personal beliefs about (moral) responsibility (Synofzik, Vosgerau, & Newen, 2008b) as well as self-efficacy and self-esteem, as an attitude toward the self (Bandura, 1982, 2001; Skinner, 1996).

Synofzik and colleagues (2008b) consider personal beliefs about responsibility to be a meta-representation of the self, in particular, a representation of its capacity to influence the body and (through the body) the external world. It is thought to form the highest cognitive dimension of agency experience. A disturbance at this level is reflected in exaggerated belief of responsibility for preventing negative events for example in obsessive-compulsive disorder (Moulding & Kyrios, 2006; Salkovskis, Shafran, Rachman, & Freeston, 1999). The ascription of self-responsibility has been proposed to depend on an individual’s awareness of a will underlying the action, the potential action outcomes, contextual barriers and, in the case of moral responsibility, social norms (Synofzik, Vosgerau, & Newen, 2008b).

1.2 Cues to agency

The perception of causality in general has been shown to rely on the detection of spatio-temporal correlations between two events A and B, for example the movement of an object A and the movement of an object B (e.g., Elsner & Hommel, 2004; Michotte, 1963; Shanks & Dickinson, 1987). Agency as a special case of causation differs in that event A is oneself, that is the will, and event B is the bodily movement, or alternatively, event A is the bodily movement (e.g., pushing a button on the phone) and event B is an event in the external world (e.g., a sound). That is, in both cases the observation of event A consists of a representation of self-related information, namely the will or the movement command, which is accessible prior and in addition to the perception of external effects. Two models of agency have received extensive empirical support, the comparator model (Frith, Blakemore, & Wolpert, 2000a) and the theory of apparent mental causation (Wegner, 2003). The theories differ with respect to the emphasis on motor signals or thoughts (e.g., intentions) as the content of the reference event (A) that is used for establishing a causal relation with the effect (event B).

1.2.1 Motor signals

The comparator model or predictive account (see Fig. 1; Sato & Yasuda, 2005; for a critical discussion see Synofzik, Vosgerau, & Newen, 2008a) claims that the sense of agency depends on a comparison between *predictions* made by an internal model of the motor system, a so-called forward model and sensory signals resulting from the corresponding action (Frith, Blakemore, & Wolpert, 2000a; Georgieff & Jeannerod, 1998; Sperry, 1950; von Holst & Mittelstaedt, 1950): a concordance between predictions and sensory signals would be the cue to attribute the observed effects to an internal source, a mismatch would lead to an external attribution.

The impact of motor predictions on the sense of agency has been demonstrated using different measures of agency such as explicit judgments (e.g., Sato & Yasuda, 2005), sensorimotor attenuation (e.g., Blakemore, Frith, & Wolpert, 1999; Lindner, Thier, Kircher, Haarmeier, & Leube, 2005) or intentional binding (e.g., Moore & Haggard, 2008; Voss et al., 2010; for a description of measures, see chapter 1.3). However, since internal motor signals operate primarily at an automatic level and have been demonstrated to be poorly accessible to conscious awareness, they are more accurately reflected in implicit measures such as kinematics than explicit judgments of action (Fourneret & Jeannerod, 1998; Georgieff & Jeannerod, 1998). Typical experimental approaches for studying motor predictions include the gradual distortion of action feedback in time or space (e.g., Leube et al., 2003), the comparison of active and passive movements (e.g., Engbert, Wohlschläger, & Haggard, 2007) or the variation of outcome probability (e.g., Moore, Lagnado, Deal, & Haggard, 2009).

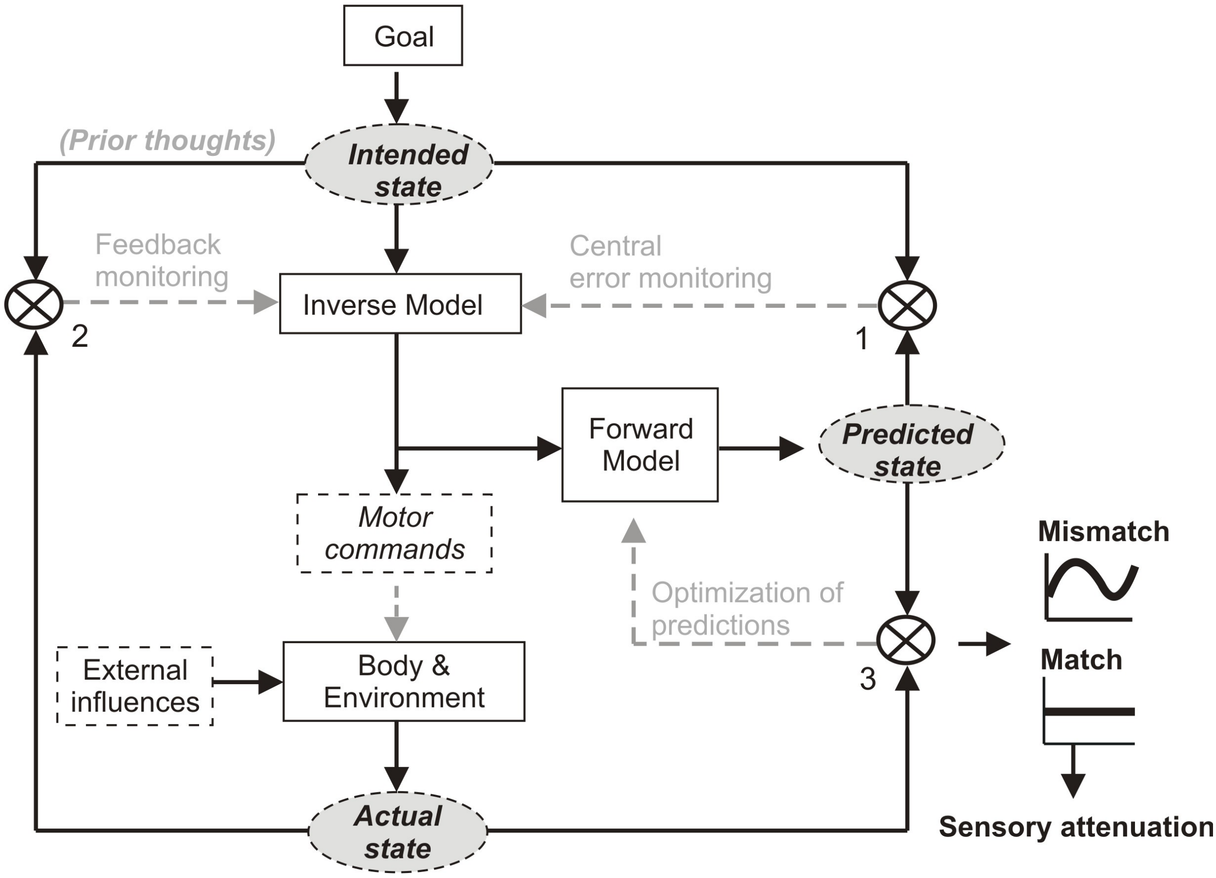


Figure 1.1. The comparator model of the sense of agency. This model is based on a framework of the motor control system that postulates three different representational states of the system: the intended state, the predicted state and the actual state. During action, a forward model based on action-related signals predicts the sensory consequences of the action. This sensory prediction is used for online control of movements (comparator 1) and for cancellation of sensory input that is self-produced (comparator 3). The actual sensory consequences of an action can be used for feedback-based goal-directed learning (comparator 2). Adapted from Synofzik (2008a).

1.2.2 Prior thoughts

The theory of apparent mental causation or inferential account (Wegner, 2003; Wegner & Wheatley, 1999), in contrast, holds that agency is experienced only when one infers that an action was caused by one's own *thought* preceding the action. This inference is assumed to occur according to three principles: the thought appears prior to the action (priority), is consistent with the action (consistency) and no alternative causes are present (exclusivity). Experiments testing this theory typically use priming to manipulate the content of thoughts prior to an action. Priming refers to a change in the ability to process a stimulus (e.g., the sensory consequence of an action) as a result of a specific prior experience with the same, or a related, stimulus (Tulving & Schacter, 1990). The enhancing effect on the sense of agency has been shown for auditory priming (Wegner, Sparrow, & Winerman, 2004; Wegner & Wheatley, 1999) as well as for visual priming (e.g., Aarts, Custers, & Wegner, 2005; Linser & Goschke, 2007). Most of these studies used explicit agency judgments but some also employed implicit measures such as sensorimotor attenuation (e.g., Sato, 2009) and intentional binding (e.g., Moore, Wegner, & Haggard, 2009). Furthermore, it has been shown that both subliminal stimuli and supraliminal stimuli are equally effective, meaning that agency experience can be influenced by conscious and unconscious anticipatory representations of the action effect (Linser & Goschke, 2007). This suggests an underlying automatic process for which prior thoughts need not be conscious to serve as a reference signal for inferring agency.

1.2.3 Integration of multiple cues

Instead of being mutually exclusive, however, the two models described above should be considered as complementing each other. Recent integrative frameworks assume that multiple cues contribute to the sense of agency depending on the level of representation, for example feeling versus judgment of agency (see Fig. 2, Synofzik, Vosgerau, & Newen, 2008a, 2008b), or on the level of intention, distal, proximal or motor intention (Pacherie, 2008).

Synofzik and colleagues (2008b) propose that at a lower level, motor predictions and reafferent feedback from vision and proprioception (Tsakiris & Haggard, 2005) are necessary conditions for a feeling of agency. At a higher level, judgments of agency are formed by integrating these low-level sensorimotor signals into a cognitive system of intentions and personal theories that are based on prior experience in certain psychosocial contexts and cultural knowledge (see also Young, 1995). It has been further proposed that these different agency cues are optimally combined to obtain the most robust estimate of self-causality (Synofzik, Vosgerau, & Lindner, 2009). In particular, it is assumed that different cues may outweigh or even substitute each other depending on their relative reliability and availability in a certain context (Moore, 2009). For example, the presence of potential alternative agents may change the weighting of internal signals: when a nearby glass falls on the floor, the fact of being alone in the room may be informative enough, whereas internal sensorimotor cues would receive more weight if other people were around.

Evidence for optimal cue integration underlying the sense of agency is still scarce, in particularly concerning the interaction of cognitive cues (such as prior thoughts or context) with sensorimotor signals. One goal of the present research was to shed light on the mechanisms of cue integration at different levels of agency processing.

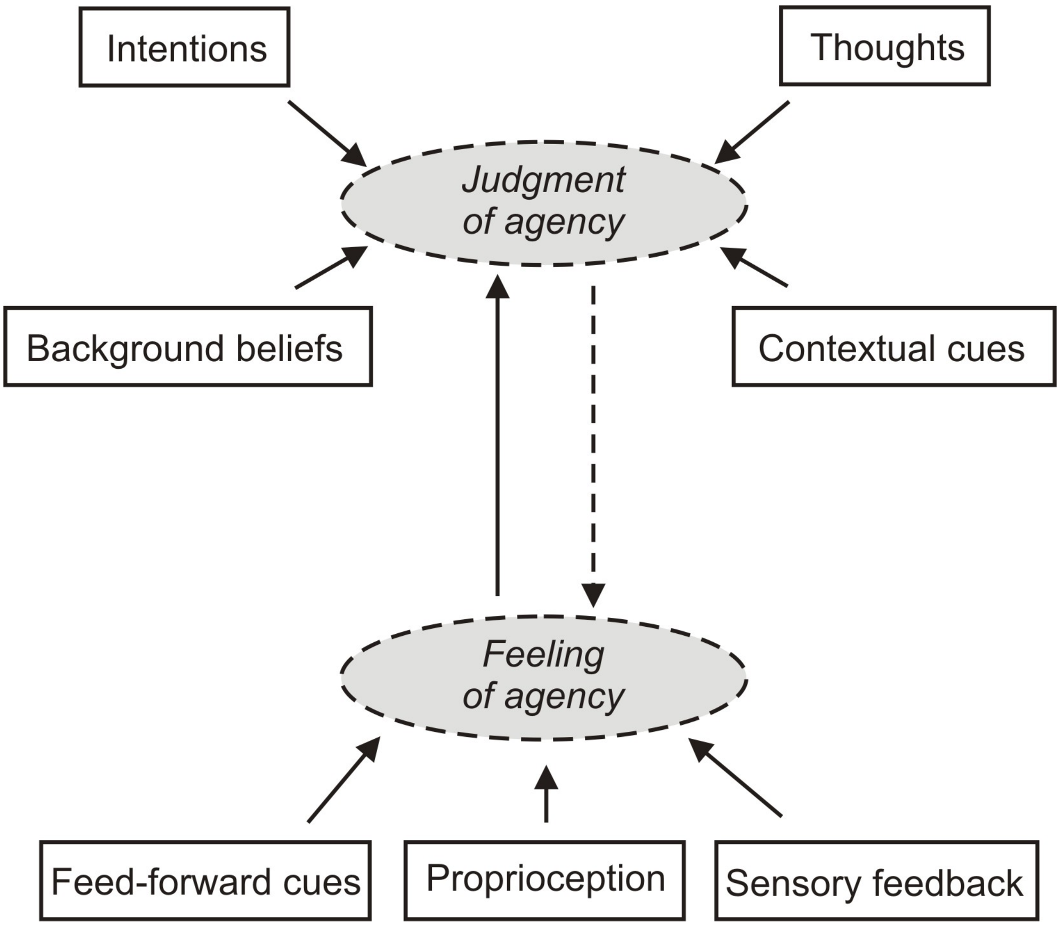


Figure 1.2. The account of an optimal cue integration underlying the sense of agency. This framework assumes that a combination and integration of multiple cues provides the basis for a robust and flexible agency experience in variable contexts. Two representational levels of agency experience are distinguished: the feeling of agency and the judgment of agency. The weighting process of cognitive, perceptual and motor cues is thought to differ between the two levels. Adapted from Synofzik (2008a)

1.3 Measures of the sense of agency

Current experimental measures and paradigms also are highly diverse due to different operational definitions of the concept of agency. Two different approaches can be distinguished: explicit measures involving verbal judgments of agency and implicit measures capturing phenomenological and neural reflections of agency.

1.3.1 Agency judgments as an explicit measure

Judgments of agency are typically assessed following free- or forced choice button presses or simple movements (e.g., a single-finger extension, hand gestures or rotations of a joystick). In some studies, participants are asked to indicate the degree of felt control or intention for such actions (Linser & Goschke, 2007; Wegner, Sparrow, & Winerman, 2004; Wegner & Wheatley, 1999) or to attribute a visual action effect to a particular agent, for example to themselves, the computer or another person (Aarts, Custers, & Wegner, 2005; Sato, 2009; Sato & Yasuda, 2005). Typically these judgments are made on visual analogue scales (10-points or 100-points) ranging from *not at all me* to *absolutely me,* or from *I allowed it to happen* to *I intended to make it,* or from *no control* to *complete control*. In other studies, participants have to judge the image of a movement displayed on a computer screen. These judgments typically involve *Yes* or *No* to indicate whether the image was spatio-temporally concordant with their own movement (Farrer, Franck, Paillard, & Jeannerod, 2003; Leube et al., 2003) or whether they saw their hand or someone else's hand on the screen (Daprati et al., 1997; Sirigu, Daprati, Pradat-Diehl, Franck, & Jeannerod, 1999; Tsakiris & Haggard, 2005).

However, as stated earlier, explicit measures are not able to capture the content of the agency experience that accompanies most of our everyday actions, namely the feeling of harmonious flow from our thoughts to our actions to the sensory consequences in the world which induces a sense of effectiveness and completion during an action (see chapter 1.1.2). Aspects of this feeling of agency can be targeted by different implicit measures.

1.3.2 Sensory attenuation as an implicit measure

An implicit measure has the potential to access mechanisms of automatic information processing underlying a cognitive function more directly than subjective judgments. Different implicit measures of the sense of agency have been proposed: The *kinematics* of a movement, for example, can reveal the properties of an underlying action program and monitoring mechanism which cannot be verbally reported. For example, the detection of small deviations of an outcome from an intended action outcome may be reflected in adjustments of movement that remain unconscious (Fourneret & Jeannerod, 1998; Knoblich & Kircher, 2004). *Intentional binding* is another implicit measure which captures representations of the temporal relation between actions and effects. For example, the perceived timing of an external effect changes (i.e., it is perceived as occurring earlier) specifically if the effect follows a voluntary action which aims at producing it (Haggard, Clark, & Kalogeras, 2002). In the focus of the present research, however, there is yet another implicit measure which has been termed *sensory attenuation (Blakemore, Wolpert, & Frith, 2000; or alternatively: sensorimotor attenuation, sensory suppression, sensory gating, corollary discharge signal or reafference principle)* and will be described in more detail in the following.

Sensory attenuation is the product of a physiological mechanism that specifically predicts and filters the consequences of one's own actions, for example the sensory input to the skin when one is grasping a glass of water. Von Holst and Mittelstaedt (1950) pointed out that it reflects a distinctive feature of "reafference" (i.e., sensory input resulting from one's own movements), as compared to "exafference" (i.e., sensory input resulting from occurrences in the environment): reafferent input cancels and neutralizes with an "efference copy" (i.e., a copy of the motor command) or a corollary discharge (Sperry, 1950) that is issued to the sensory pathway. This mechanism allows the central nervous system to resolve the confusion between simultaneous reafferent and exafferent input during movement, and it has been described for various species and different sensory modalities (Crapse & Sommer, 2008).

The result of this cancellation in vision, for example, is the impression of a stable external world despite the constantly changing visual input caused by our eye movements (e.g., Wurtz, 2011). In the perception of touch, an example is the phenomenon that one cannot tickle oneself (Blakemore, Frith, & Wolpert, 1999; Weiskrantz, Elliott, & Darlington, 1971): specifically, self-produced tactile stimulation is perceived as being less tickly, intense and pleasant than an identical stimulus produced externally. In this way, self-generated sensory events are associated with a specific perceptual quality. Modern views of this principle proposed by von Holst and Sperry include a forward model which captures the causal relations between movements and their bodily or environmental outcomes and thereby serves as a predictor of sensory input (Wolpert & Ghahramani, 2000; Wolpert, Ghahramani, & Jordan, 1995). These internal predictions are used for fine adjustments to ongoing motor commands, and they can also be used for a comparison with the actual sensory effects of movement which are attenuated in case of a match. Since the comparison between predicted and actual sensory input lies at the core of the comparator model of the sense of agency (e.g., Sato & Yasuda, 2005; see chapter 1.2.1), sensory attenuation, in the light of this model, can be considered the primary measure for agency experience.

Various methods have been used for measuring sensory attenuation such as psychophysical perceptual estimates (e.g., Blakemore, Frith, & Wolpert, 1999) and behavioral measures (e.g., Shergill, Bays, Frith, & Wolpert, 2003) as well as recordings of neural activity (e.g., Houde, Nagarajan, Sekihara, & Merzenich, 2002). In the present research, we used event-related brain potentials (ERPs) of electrophysiological recordings in which sensory attenuation has been repeatedly observed around 100 ms following the occurrence of a self-produced sensory event, specifically, in the N1 component (Ford & Mathalon, 2004; Heinks-Maldonado et al., 2007; Lange, 2011; Schafer & Marcus, 1973). Furthermore, the implicit measure of sensory attenuation was combined with an explicit measure of causality judgment in order to gain a broader and more comprehensive picture of the sense of agency, its subcomponents and their possible impairment in obsessive-compulsive disorder.

1.4 Pathologies of the sense of agency: Obsessive-compulsive disorder

There are different pathological disruptions of agency. Typically, schizophrenia patients with delusions of control have been discussed in this context (e.g., Frith, Blakemore, & Wolpert, 2000b) but also neurological symptoms, including anarchic limb sign or anosognosia for hemiplegia (e.g., Synofzik, Vosgerau, & Newen, 2008b). The focus of the present research is obsessive-compulsive disorder, a pathology that has so far been largely neglected.

Obsessive-compulsive disorder (OCD) is characterized by recurrent thoughts that are unwanted, distressing and insistent (i.e., *obsessions*), and urges to perform mental or physical acts repeatedly, in ritualistic, stereotyped succession (i.e., *compulsions*), both of which significantly impair everyday functioning (American Psychiatric Association, 1994). Common contents of obsessive thoughts involve self-doubt (e.g., whether a certain behavior was done, and done just right, such as turning off the stove), contamination (e.g., that hands are still dirty after washing them) and symmetry (e.g., that objects are not lined up properly). Common compulsive acts include repeated checking (e.g., going back over a behavior such as turning off the stove repeatedly), washing (e.g., excessive washing of hands) or ordering (e.g., to line up the books on the shelf over and over). Compulsions are considered responses to particular obsessions aiming to relief the negative affect (i.e., anxiety, uncertainty) or to prevent harm to oneself or others which might be related to obsessions.

Cognitive theories of obsessions suggest that beliefs about responsibility for causing or preventing harm are a critical factor in the maintenance of compulsions and other forms of neutralizing behavior (Rachman, 1997; Salkovskis, Shafran, Rachman, & Freeston, 1999). However, recently it has been criticized that existing research has focused too strongly on patients' cognition about intrusions or on overt neutralizing behavior and has largely neglected a phenomenological approach for understanding OCD (Ecker, 2002). The phenomenology of obsessions and compulsions refers to the subjective inner experience during symptom expression which is often difficult to verbalize. An example is the experience of dissatisfaction and incompleteness related to an action and the "need for experiences to conform to exact, yet often inexpressible criteria" (Summerfeldt, 2004, p.1156).

The role of incompleteness feelings in the phenomenology of OCD has already been recognized 1903 by Pierre Janet (Pitman, 1987b) and recently been re-conceptualized as "not just right experiences" (Coles, Frost, Heimberg, & Rheaume, 2003) or as persistent internal error signals and impressions of something being wrong with an action (Aouizerate et al., 2004; Pitman, 1987a; Schwartz, 1998). In fact, neuroimaging research confirmed hyperactivity of brain regions sensitive to response errors and conflict, specifically in basal ganglia-thalamo-cortical loops involving the medial frontal cortex (MFC), that is, the anterior cingulate cortex and premotor regions (e.g., Gehring, Himle, & Nisenson, 2000; Saxena, Brody, Schwartz, & Baxter, 1998; Ursu, Stenger, Shear, Jones, & Carter, 2003; Yucel et al., 2007). These results indicate a dysfunction in the processing of action outcomes in OCD.

Established models of motor control, however, indicate that several kinds of motor representations and monitoring processes take place to evaluate actions and their outcomes (Frith, Blakemore, & Wolpert, 2000a; Wolpert, 1997; see Fig. 1). A first comparator monitors for goal-achievement using representations of the intended and predicted action outcome. A second comparator enables feedback-based action learning based on representations of the intended and actual outcome. A third comparator evaluates the precision of forward model predictions and reflects the degree of causation and control (i.e., agency) for an outcome. These different components of motor control have been related to different neural systems (Krigolson & Holroyd, 2006; Wolpert & Ghahramani, 2000), however, OCD research so far exclusively focused on comparators 1 and 2. In order to gain a more comprehensive and complete picture of the outcome processing deficit in OCD, the functional integrity of forward models underlying the third comparator should be investigated. Abnormalities in this specific monitoring mechanism would indicate a disturbed feeling of agency as suggested by the phenomenological feature of incompleteness in these patients.

2 Summary of Experimental Studies

2.1 General objectives

The overall aim, which was characteristic for all studies that contributed to the present work, was to combine explicit and implicit measures for investigating processes underlying feelings and judgments of agency respectively. Typically, research exploring the mechanisms by which the experience of oneself as an agent is generated focuses only on one particular aspect of agency, namely, the way people make explicit attributions about who or what might be the most plausible cause for a sensory event in a given situation. These explicit judgments, however, do not reflect the feeling of agency which accompanies our actions by default and which can be accessed only by indirect, implicit measures that are not based on verbal reports or conscious decisions.

A second general objective across the different studies that were conducted was to test predictions of a recent integrative account of agency (Synofzik, Vosgerau, & Lindner, 2009; Synofzik, Vosgerau, & Newen, 2008b), for which evidence is still scarce. As described in chapter 1.2.3, this theory proposes a weighting and integration of different agency cues depending on their relative reliability and depending on whether a feeling or judgment of agency is formed. In two subsequent studies (Study 1 and 2) involving healthy participants the integration of three important agency cues was investigated: first, the presence of motor signals, second, anticipations due to prior thoughts and, third, the availability of precise motor predictions.

A third important objective of this research was to explore mechanisms of agency formation in individuals suffering from OCD, which was realized in Study 3. Until now, no investigation of the sense of agency has been conducted in a clinical population of OCD patients, despite its phenomenological plausibility and despite the possibility to gain a broader view on the motor control deficit that has often been implicated in this disorder (e.g., Gehring, Himle, & Nisenson, 2000). Furthermore, studying psychopathological conditions in which particular aspects of the sense of agency are disturbed may provide deeper insights into the nature and interrelation of different components of the agency experience, such as sensorimotor and higher-order cognitive processes.

2.2 Summary of Study 1

Prior thoughts have been proposed to act as an important agency cue if they concord with the action outcome. Although this has been demonstrated for explicit judgments of agency, little is known at the level of feeling of agency about the effects of such cognitive cues in general and how they interact with sensorimotor cues. The objective of Study 1 was to examine the influence of both prior thoughts and motor signals on sensory attenuation, a marker of the feeling of agency in early sensory processing of action outcomes. ERPs were recorded while participants performed a causality judgment task in which visual sensory effects were either produced by an action or by the computer. Prior thoughts were manipulated by subliminally priming the visual effect prior to action with congruent, incongruent or neutral stimuli. Study participants were 20 healthy subjects recruited from the general community, and the experiment was conducted at Max-Planck Institute for Human Cognitive and Brain Sciences, Leipzig. The main outcome measures included causality judgments on a visual analogue scale ranging from 0 ("no control") to 100 ("full control") and the visual N1 component relative to the occurrence of the visual effect.

Our results revealed a reduction in amplitude of the visual anterior N1 component for self-generated effects as compared to externally generated effects. Moreover, congruent primes enhanced causality judgments and further reduced N1 amplitudes relative to neutral or incongruent primes, however, only if the effect was produced by an action and not just passively observed. These data show sensory attenuation in early visual processing of action outcomes indicating the presence of a feeling of agency for self-caused external visual effects. Furthermore, the results support the role of prior thoughts not only in the formation of a conscious agency judgment but also in the generation of a feeling of agency, however, depending on the presence of motor signals. More generally, these findings imply top-down influences of cognitive agency cues on lower-level processes of sensorimotor integration.

[The manuscript of Study 1 is to be found from pages 31 to 58]

2.3 Summary of Study 2

The sense of agency has been shown to depend on accurate anticipation of an action outcome based on precise internal motor predictions or based on prior thoughts concerning the action effect. It has been proposed that these cues are weighted and integrated according to their relative reliability and depending on the level of agency registration. The objective of Study 2 was to test the hypothesis of optimal cue integration underlying the judgment and feeling of agency for these specific agency cues. A modified version of the experimental paradigm used in Study 1 was employed. During EEG recording, participants either actively produced or passively observed visual effects which were highly contingent (75%) upon their action or not (50%), and which were primed prior to action with congruent or incongruent stimuli. Study participants were 23 healthy subjects recruited from the general community, and the experiment was conducted at Max-Planck Institute for Human Cognitive and Brain Sciences, Leipzig. The main outcome measures included analyses of causality ratings and N1 component of the ERP to the visual action effects.

The results showed that participants judged agency to be larger during congruent than incongruent priming conditions, however, only if action-effect contingency was low. Causality judgments during passive observation were slightly enhanced by congruent primes, only if contingency was high. Visual anterior N1 responses to self-produced effects were dampened relative to N1 to externally produced effects, and this was most pronounced if effects were preceded by congruent primes independent of the degree of action-effect contingency. N1 amplitudes to externally produced effects were also reduced by congruent priming, again only if contingency was high. N1 was unaffected by contingency. Together, the data of Study 2 supports the hypothesis of optimal cue integration underlying the sense of agency. Specifically, agency judgments most strongly depend upon precise motor predictions, and prior thoughts only have an impact if these predictions are not reliable enough or in the absence of any embodied signals. Sensory attenuation, in contrast, is based on the mere presence of embodied signals and on prior thoughts, independent of precise motor predictions. These findings suggest that processes of cue weighting and integration differ between levels of agency registration.

[The manuscript of Study 2 is to be found from pages 59 to 82.]

2.4 Summary of Study 3

The phenomenology of obsessive-compulsive disorder (OCD) suggests a disruption in agency experience however very little empirical research has been conducted on this topic. Peculiar sensory phenomena such as a lacking sense of action completion and the need to re-enact certain actions may be associated with an undermined feeling of agency due to deficient processes of sensorimotor integration. The objective of Study 3 was to explore brain responsiveness to sensory action effects in OCD patients, in particular by measuring sensorimotor attenuation as a marker of the pre-reflective feeling of agency. Moreover, higher-level judgments of agency were examined in order to obtain a comprehensive picture of agency processing in OCD.

A modified version of the causality judgment paradigm used in Study 2 was employed during EEG recording, consisting of visual color stimuli that were either self- or externally generated, highly contingent (75%) or not contingent (50%) upon the action, and primed with congruent or incongruent color words. Study participants were 18 patients with OCD recruited from the academic outpatient department for OCD at Humboldt-University Berlin, and 18 age- and sex-matched control subjects recruited from the general community. The experiment was conducted at Humboldt-University Berlin. The main outcome measures included analyses of the visual N1 component of the ERP, causality judgments and psychometric measures of symptom severity.

In healthy controls, the posterior N1 component was found to be attenuated to self- relative to externally produced effects, and further reduced to highly contingent relative to non-contingent action outcomes. This pattern was not seen in OCD patients. Furthermore, causality judgments were slightly enhanced in OCD patients as compared to healthy controls and larger for highly contingent as compared to non-contingent outcomes in both groups. Congruent prime stimuli enhanced agency judgments for highly contingent outcomes, however, only in controls but not in patients. Together, these data demonstrate deficient sensory suppression in OCD suggesting an imprecision of forward model predictions of the motor system which prevents the cancellation of sensory action consequences. This may explain the patients' need to re-enact certain actions until a satisfying outcome has been obtained signaling task completion. The tendency of OCD patients to consciously perceive enhanced agency may reflect a compensatory mechanism for restoring a threatened sense of self at lower levels. In conclusion, the findings of Study 3 emphasize a disturbance of the sense of agency in OCD which should be incorporated into contemporary theories.

[The manuscript of Study 3 is to be found from pages 83 to 106.]

3 General Discussion

3.1 Attenuation in sensory perception and the sense of agency

The present research focused on the sense of agency that one can have for extracorporeal events in the *external* world, in particular for *visual* events. In everyday life, for example, one may experience agency for a colored line that appears when passing a paint-brush over a blank paper. An immediate feeling of agency may emerge in this case without conscious reflection about it, and a marker for investigation of this feeling has been sensory attenuation. In recent years, cognitive neuroscience has elucidated some of the mechanisms underlying this sensory attenuation, focusing however on tactile and auditory modalities (e.g., Blakemore, Wolpert, & Frith, 1998; Houde, Nagarajan, Sekihara, & Merzenich, 2002). One of the values of the present work is that it extends this research to the visual modality by showing self-specific attenuation at visual cortical level, which was replicated across three studies. Specifically, the N1 component of the visual ERP was found to be reduced in amplitude when a stimulus was self-generated and not externally produced.

Our findings of self-specific N1 attenuation resemble reports of N1 suppression to self-generated sounds in the auditory modality (e.g., Lange, 2011; Martikainen, Kaneko, & Hari, 2005). Functionally, the visual N1, like the auditory N1, is thought to reflect processes of active filtering and has been found to emanate from sensory cortical structures (Martinez et al., 1999). Across studies, sensory attenuation at different latencies and topographies was observed: in Study 1 and 2 it appeared around 100ms in the early anterior N1 (N1a), and in Study 3 around 150ms in the later posterior N1 (N1p). It has been suggested that specifically N1p reflects discriminative processes: a larger N1p is observed when stimuli have to be discriminated according to certain features such as color or form (Vogel & Luck, 2000). These authors also observed a slightly larger N1a during discrimination of form as compared to color however the difference did not reach significance. One can only speculate that in the present paradigm form discrimination (Study 1 and 2) was reflected in N1a activity, and color discrimination (Study 3) in activity of N1p. In general, more research is needed to systematically disentangle visual N1 subcomponents and their specificities in information processing within one experimental paradigm in order to be able to interpret functional dissociations between components.

The visual N1 has mostly been studied in the context of spatial attention and suggested to reflect the selective amplification of information that appears in attended locations (for a review, see Mangun, 1995). Importantly, in the present studies all stimuli required active discrimination and appeared at attended locations, hence nonspecific effects of spatial attention cannot explain the observed attenuation. Instead, it has been proposed that sensory attenuation is due to a precise cancellation of action effects, based on specific sensory predictions of the motor system, with the amount of attenuation being proportional to the congruence of predicted and actual feedback (Blakemore, Frith, & Wolpert, 1999; Blakemore, Wolpert, & Frith, 1998, 2000). However, while it is accepted that attenuation depends on motor predictions, the precision of these predictions remains debated (Lange, 2011; Tsakiris & Haggard, 2003, 2005).

In Study 1 and 2 precise sensory expectations were induced independently of the motor system using priming and were found to modulate N1a amplitudes. In contrast, in Study 2 and 3, the precision of motor predictions was manipulated by varying the degree of action-effect contingency however the two studies yielded discrepant results. That is, only in Study 3 the N1p attenuation was observed to be proportional to the error of motor predictions. The absence of an effect in Study 2 may have been due to reduced reliability of internal predictions in a context of frequent alternation between high and low contingency as compared to a context of longer exposure to a certain degree of contingency (Study 3). Alternatively, certain features of a stimulus may be more salient if they change, for example deviations in color (as in Study 3) have been shown to elicit memory-based components more robustly than changes in form or orientation (as in Study 2) (Czigler, Balázs, & Winkler, 2002; Pazo-Alvarez, Cadaveira, & Amenedo, 2003). In fact, the way in which top-down expectations are integrated at different levels of (visual) sensory processing is an emerging and unresolved issue in current cognitive neuroscience (see, e.g., Bubic, von Cramon, & Schubotz, 2010; Pazo-Alvarez, Cadaveira, & Amenedo, 2003; Summerfield & Egner, 2009).

Together, our findings suggest that self-specific sensory processing as reflected in attenuated brain activity during early visual perception is primarily based on the presence of embodied signals and may benefit from precise sensory predictions if they are available and reliable. In other words, the immediate feeling of agency for an extracorporeal visual event relies on the observer's private access to internal states which is available before external feedback from the movement arrives. Furthermore, the present research contributes to the understanding of the temporal dynamics and neuroanatomy of the sense of agency. The high temporal resolution of ERPs reveals the time course of self / non-self distinction: at the cortical level, the brain begins to perform automatic, differential processing of sensations caused by oneself or externally within 100 to 150 ms after onset of the sensory event. The specific perceptual quality of self-generated sensations which results from this early mechanism may give rise to the pre-reflective feeling of agency as a first cue to self-causality.

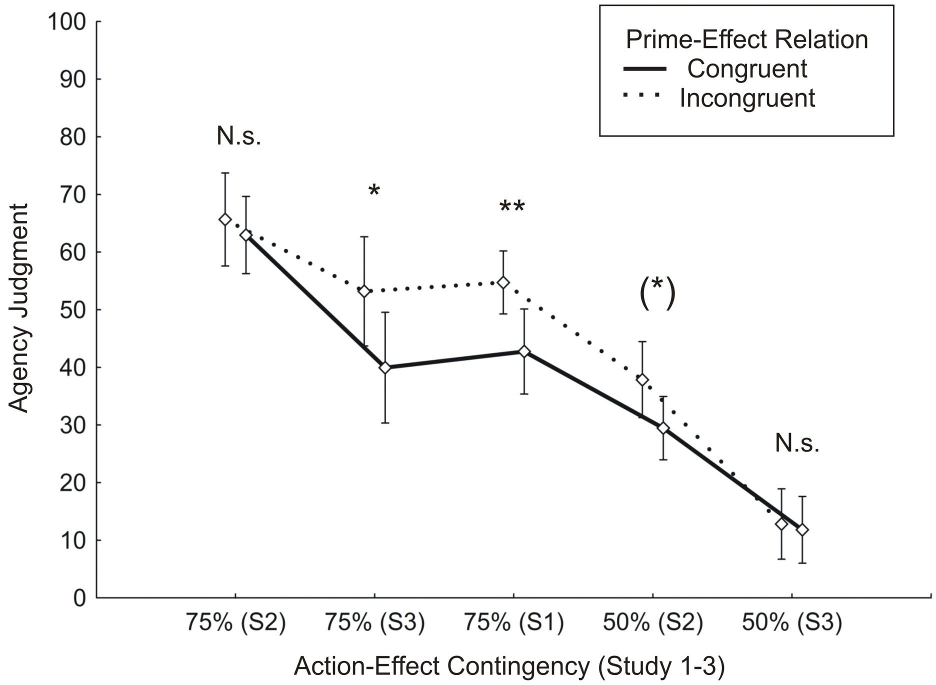
The source of the corollary discharge underling sensory attenuation has been ascribed to different cortical and subcortical motor areas, depending on the type of action, such as supplementary motor area (e.g., Haggard & Whitford, 2004; Voss, Ingram, Haggard, & Wolpert, 2006), cerebellum (e.g., Blakemore, Frith, & Wolpert, 2001; Blakemore, Wolpert, & Frith, 1998) or superior culliculus (e.g., Wurtz, McAlonan, Cavanaugh, & Berman). The anticipation associated with this corollary discharge has been shown to affect the interpretation of sensory input in primary sensory cortices (somatosensory: e.g., Blakemore, Wolpert, & Frith, 1998; auditory: e.g., Houde, Nagarajan, Sekihara, & Merzenich, 2002; visual: e.g., present research) as well as in higher sensory and association cortices (occipital: e.g., David et al., 2007; parietal: e.g., Farrer et al., 2003; temporal: e.g., Leube et al., 2003).

By contrast, imaging studies trying to map conscious judgments of self versus external causation point towards higher cognitive areas such as the prefrontal cortex being involved in processes of belief formation and goal evaluation (for review, see David, Newen, & Vogeley, 2008; Slachevsky et al., 2001). For example, medial and lateral prefrontal cortices have been implicated in monitoring for goal achievement (Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004; Schnell et al., 2007) and self-referential processing (for a critical review, see Gillihan & Farah, 2005; e.g., Gusnard, Akbudak, Shulman, & Raichle, 2001). Thus, it seems that different aspects of the sense of agency may be mapped onto distinct neural correlates. The agency experience may be built in stages, as has been proposed recently for the self: from primordial feelings generated in the brain stem to a core self and autobiographical self in the cerebral cortex (Damasio, 2010). Alternatively there may be an assembly of different aspects of agency experience that are based on very specific information-processing mechanisms. The precise identification and description of the interaction among these aspects, for example between higher cognitive control beliefs and low-level sensorimotor processes, remains a central topic and challenge for empirical investigation.

3.2 Optimal integration of agency cues

The results of the present three studies provide direct support for the hypothesis that a robust experience of agency is established by an optimal combination of different cues, instead of relying on a single source of information (Moore, Wegner, & Haggard, 2009; Synofzik, Vosgerau, & Lindner, 2009). More specifically, the present research shows that embodied signals, motor predictions and cognitive cues in the form of prior thoughts are weighted against each other, and are recruited depending on their reliability and availability in a certain context. Moreover, the present findings reveal that the weighting of agency cues differs between the levels of feeling and judgment of agency. Figure 3.1 gives an overview of the causality judgments obtained in the present three studies.

Explicit agency judgments were primarily influenced by the degree of action-effect contingency, which is in line with findings from recent studies (Moore, Lagnado, Deal, & Haggard, 2009; Sato, 2009). Specifically, if precise predictions of the external sensory event on the basis of the selected action turned out to be accurate, agency for the sensory event was judged to be high. Thus, our results confirm the role of contingency as a critical source of information for estimations of causality in general, that is, for the perception of self-causality (see Fig. 3.1A; Elsner & Hommel, 2004; Frith, Blakemore, & Wolpert, 2000a), as well as for perceiving causality between external events (see Fig. 3.1B; Michotte, 1963; Shanks & Dickinson, 1987). Importantly, the assignment of weight to this cue however varied depending on its contextual salience. Action-effect contingency appeared to be more informative in contexts of rapidly changing conditions of low and high contingency (Study 2), which possibly increased its salience as a potential agency cue, as compared to contexts of rather constant conditions of high or low contingency (Study 1 and 3).



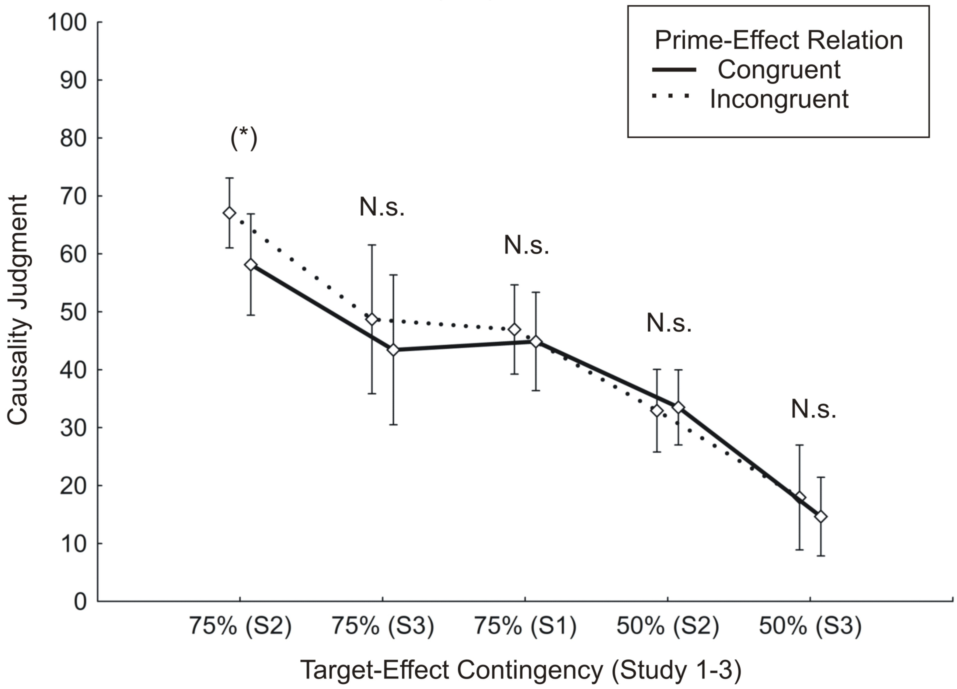


Figure 3.1. (A) Mean agency judgments in the ME task and (B) mean causality judgments in the E task as a function of prime effect relation (congruent, dotted line; incongruent, solid line). Conditions of high contingency (75%) and low contingency (50%) are plotted on the abscissa separately for Study 1 (S1), Study 2 (S2) and Study 3 (S3). Vertical bars indicate 95% confidence intervals. Asterisks show significant differences between the priming conditions (**P < 0.01; *P < 0.05; (*) P < 0.10; n.s., not significant)

As to the influence of prior thoughts, it was observed that subjects' reliance on this cognitive cue for an explicit agency estimate was a function of the reliability of alternative embodied cues and the uncertainty in a given context. That is, prior thoughts operated only as agency cues within a certain window of agency ambiguity as perceived by the subject and as reflected in mean estimates of causality around 50 on the visual analogue scale ranging from 0 to 100. In contexts of high agency ambiguity due to unreliable contingency information, primes received relatively more weight as compared to contexts in which contingency was perceived as being a highly informative cue for an estimate of agency (Fig. 3.1A, left). Moreover, primes received less weight in contexts in which embodied cues were completely unreliable (Fig. 3.1A, right) or unavailable (Fig. 3.1B) suggesting that prior thoughts as a cognitive agency cue are only recruited in the presence of embodied signals.

At the level of feeling of agency (as measured by sensory attenuation), in contrast, weighting and integration of the same agency cues appeared to be different. Study 2 and 3 demonstrate that the mere presence of motor signals may have more impact on the feeling of agency than specific contingency information. Moreover, findings of Study 1 and 2 reveal that prior thoughts can operate as an additional cognitive cue depending on the presence of embodied signals, however, independent of contingency information. In fact, with regard to the role of contingency as a potential agency cue at this level of agency registration, Study 2 and 3 yielded discrepant results. This discrepancy mirrors the controversy in the current literature on the precision of the motor predictions underlying sensory attenuation (Lange, 2011; Tsakiris & Haggard, 2003; see also chapter 3.1). Hence, the feeling of agency seems to be primarily informed by embodied signals (i.e., the presence of efference), and may be further influenced by cognitive cues and detailed predictions made by forward models, when available.

Together, the present research shows that the sense of agency for an extracorporeal event depends on the presence of an action, on contingency knowledge, and on the content of thoughts prior to the action. The impact of each of these cues seems to depend on their relative reliability, availability or salience in a specific context. While our findings lend support to the proposal of cue integration underlying the sense of agency, the operations of this integration process need to be tested further, in particular, the reliance on Bayesian rules of optimal weighing of sources according to their relative uncertainties (Kording & Wolpert, 2006). There is strong potential for cognitive psychology and neuroscience to generate further insight to this end, especially if combined with paradigms that allow a more direct manipulation of contextual priors or the investigation of the acquisition of agency experience for new sensory events.

3.3 A disturbed sense of agency in obsessive-compulsive disorder

A key finding from the present research is the lack of sensory attenuation together with a slight increase in conscious perception of agency in patients with OCD as compared to control subjects (Study 3). This is the first systematic examination of the neurocognition of agency in OCD patients. Our results are consistent with a recent study (Rossi et al., 2005) which recorded median-nerve somatosensory evoked potentials and found hypofunctioning sensory gating in OCD patients. We extend these results by showing reduced sensory gating in OCD patients also for extracorporeal action effects and, furthermore, our findings suggest that the impairment is due to a specific deficiency in predicting the sensory consequences of actions.

It is possible to speculate that hyperactive premotor regions in OCD, such as supplementary motor area (SMA), may prevent a fine-tuning of corollary discharge and associated sensorimotor integration processes which results in an inability to modulate sensory action consequences. Indeed, areas involved in motor preparation such as the SMA have been ascribed a crucial role in supporting sensory suppression and action-effect binding (Haggard & Whitford, 2004; Moore, Ruge, Wenke, Rothwell, & Haggard, 2010; Voss, Ingram, Haggard, & Wolpert, 2006; Voss, Ingram, Wolpert, & Haggard, 2008) as well as conscious experience of action. For example, Fried et al. (1991) showed that direct electrical stimulation of the SMA causes an urge to move in the absence of overt movement. In OCD patients, there is evidence that repetitive transcranial magnetic stimulation to SMA improves clinical symptoms (Mantovani et al., 2006). The impairment in sensory gating of action consequences in OCD may become apparent in sensory phenomena such as feelings of incompleteness and internal error signals accompanying and motivating compulsive behaviors (Pitman, 1987a; Summerfeldt, 2004).

Our results of the present patient study (Study 3) have several important implications:

First, obsessive-compulsive disorder may be best understood as a disturbance of action outcome processing in general. In current models of motor control (e.g., Frith, Blakemore, & Wolpert, 2000a; Wolpert, 1997), two different comparator mechanisms depend on the precision of internal motor predictions: online monitoring of goal-achievement and online monitoring of sensory predictions. In line with this distinction, Krigolson and Holroyd (2006) proposed a hierarchy of error processing: a frontal-medial system that monitors for attainment of "high-level" goals, and a posterior-parietal system which is responsible for online, fine-tuned motor adjustments. A number of studies provide evidence for a dysfunction of the frontal-medial system in OCD (e.g., Gehring, Himle, & Nisenson, 2000). Our results extend these findings in suggesting a dysfunction also in the second comparator, that is, in the posterior-parietal error system (Krigolson & Holroyd, 2006). The investigation of unconscious adjustments in kinematics to distorted action feedback could provide a useful tool to further test the functional integrity of the posterior system in OCD.

Second, the present data shed light on the relation between low and high levels of agency experience. Our findings reveal that OCD can be considered a clinical case for a selective impairment of feeling of agency, with a largely preserved level of judgment. This implies that agency judgments do not critically depend on bottom-up sensorimotor signals but are primarily formed on the basis of prior experiences and beliefs concerning causality. However, the loss of reliable sensorimotor cues and the lack of feeling of control may motivate conscious compensatory behavior for regaining and increasing subjective causal influence, which might be reflected in enhanced explicit agency judgments as observed in the present study. Indeed, research suggests that illusions of control and excessive responsibility in OCD (e.g., Salkovskis, Shafran, Rachman, & Freeston, 1999) may reflect a compensation for a threatened feeling of control (Moulding & Kyrios, 2006; Reuven-Magril, Dar, & Liberman, 2008).

Third, our findings imply that the corollary discharge dysfunction found in schizophrenia (e.g., Ford & Mathalon, 2004) is not characteristic of a certain disorder. Delusions of control and auditory hallucinations in schizophrenia have typically been straightforwardly explained by impairment in forward models and corollary discharge (e.g., Frith, 2005; Frith, Blakemore, & Wolpert, 2000b; Kircher & Leube, 2003; Lindner, Thier, Kircher, Haarmeier, & Leube, 2005). However, we demonstrate that a disturbed feeling of agency can have differential impact on judgments depending on the cognitive system in which it is integrated. In schizophrenic patients, the interpretation of the noisy sensory signals seems to be framed by biased beliefs and delusions about causality (Heinks-Maldonado et al., 2007), whereas in OCD patients it seems to be integrated into a system searching for conscious control (Moulding & Kyrios, 2006).

3.4 Caveats and Considerations

One should be aware of some caveats when drawing conclusions from the present work. First, the limited ecological validity of laboratory agency paradigms should be kept in mind. We applied a commonly used design in which participants perform simple button presses which are followed by single sensory events such as a colored square on a computer screen in a dimly lit, acoustically shielded chamber. These paradigms bear the advantage of studying the construct of interest under experimentally controlled conditions, thus avoiding emotional arousal or engagement in other activities as potential confounding factors, and allowing the isolation of cognitive mechanisms. However, this is achieved at the cost of artificially reducing a complex, dynamic cognitive process and the external world to very few dimensions. This limits the explanatory power of the resulting models for daily life behavior and complex psychopathologies. Nevertheless, the results obtained from such basic research can serve as an evidence base for experiments with progressively greater ecological validity.

A second caveat is a terminological concern. In the present research, the terms causation and control were used interchangeably to describe agency experience due to their frequent appearance in the agency literature. However, there may be substantive distinctions to be drawn between these terms as suggested by conceptual frameworks (e.g., Pacherie, 2008; Skinner, 1996). Testable differences between these notions of agency should be addressed by future research in order to achieve conceptual clarification and integration of the various empirical results concerning the sense of agency. Moreover, the notions of self- and other-agency were not distinguished, which have been used by some authors in order to refer to attributions to the self vs. other agents (e.g., Sato & Yasuda, 2005). The present work, however, was exclusively focused on basic mechanisms of self / non-self distinction, and not on processes of observation and attribution of agency to other people.

An important methodological consideration concerns the lack of a semantic priming effect in the ERP of Study 3 which may have been obscured by our experimental design. Additional analyses revealed that neither early N1 nor late N400 or P3 components were affected by priming at the semantic level. The choice of prime-effect stimulus onset asynchrony (SOA, i.e., the time interval between prime and effect stimulus) has been shown to determine the probability of detecting an effect. For example, in the domain of language processing, semantic priming effects tend to dominate at short prime-effect SOAs (<250 ms; for a review, see Henson, 2003). In Study 3, a SOA of 650 ms was chosen to ensure comparability with stimulus timing in Study 1 and 2. Comparison with the priming literature however is limited since in these studies typically prime and effect follow each other without interference by response activity, as in the present paradigm. Hence, a shortening of the SOA would not have been possible in our agency paradigm however a larger SOA could be achieved in future experiments by including a delay of the go signal. Importantly, a delay of the action effect itself should be avoided since agency experience critically depends on temporal contiguity.

A final important caveat concerns the comparability and the generalizability the current results. Limited research is available for direct comparison with the present findings because studies differ in operationalization of self and non-self conditions and in their working definition of agency, such that in fact partly distinct mechanisms are investigated. Moreover, in the ERP, the functional significance of components may differ across modalities, hence, comparison of auditory and visual N1 attenuation should be made with caution. Furthermore, due to the heterogeneous patient sample concerning OCD symptoms in Study 3, general implications for pathophysiology and treatment can be only tentative before the specificity of the present findings with respect to clinical phenomenology has been tested.

Notwithstanding these limitations, the present research sheds new light into the dynamics of cognitive and brain mechanisms underlying the sense of agency and its dysregulation in OCD. One important objective of the present work was to combine explicit and implicit measures and thereby to extend previous studies using only verbal reports. Collectively, our findings offer validation of sensory attenuation as an implicit measure of basic, non-conceptual agency registration. Furthermore, in line with our second objective, the present studies tested an integrative account of agency (Synofzik, Vosgerau, & Newen, 2008b) and support the hypothesis that multiple cues contribute to the sense of agency depending on their relative reliability and availability. Moreover, a third objective of the present work was to study a case of possible alteration in agency experience. The present research reveals – for the first time, to our knowledge - reduced gating of extracorporeal sensory action consequences in patients suffering from OCD indicating an aberrant sense of agency in these patients which specifically concerns a pre-reflective aspect of agency processing.

3.5 Future directions

Clearly, several issues remain to be disclosed by empirical research to reach a comprehensive understanding of the subjective experience of agency and its disturbances.

Progress will be aided primarily by a deeper exploration of the existing implicit measures of agency, such as sensory attenuation, in order to have a clear understanding of the precise information processing mechanisms that they are able to capture. This will include investigating the nature and origin of sensory predictions underlying sensory attenuation and characterizing possible determinants such as type of action and kinematic parameters that are involved, modality and proximity of the action feedback or contextual variables. Progress can also be made using combinations of implicit measures, such as kinematics and sensory attenuation, for exploring the reciprocal relations between action control and perception, particularly the role of sensory gating in serving perception as well as action selection. The use of similar paradigms will be essential for comparisons across different types of data.

Studies of populations in which agency experience is enhanced should also be very informative, as this has been largely neglected so far. Research on disturbances of agency typically focus on manifestations of a reduction or complete lack of sense of agency as present in dysphoria, schizophrenia, anarchic hand syndrome or anosognostic symptoms. By contrast, narcissistic personality disorder in particular, exaggerated beliefs of responsibility in OCD or the proneness to magical thinking especially in children are examples of inflated agency experiences which may lead to new interesting insights into the formation of feelings and judgments of agency.

A further important direction for future research concerns the interdependencies between high- and low level features of agency representation. Existing theories and research in the area of human causal learning that emphasize the impact of prior knowledge and preexisting mental concepts on conscious sensory processing may be very informative (see, e.g., Buehner & May, 2004). In general, more research is needed to illuminate the mutual influences between high-level cognitive concepts, such as control beliefs or self-efficacy, and low-level processes of sensorimotor integration and motor control. This research may also help in answering the question of why self-generated, noisy sensory signals cause delusional misattributions to external sources in one person but not in others.

4 Manuscript of Study 1

I Did It: Unconscious Expectation of Sensory Consequences Modulates the Experience of Self-agency and Its Functional Signature

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Abstract

The ability to recognize oneself in voluntary action is called the sense of agency and refers to the experience of causing one's own actions and their sensory consequences. This form of self-awareness is important not only for motor control but also for social interactions and the ascription of causal responsibility. Here, we examined the sense of agency at early and pre-reflective stages of action perception using event-related potentials (ERPs) while subjects performed a visual forced-choice response task in which action effects were either caused by the subject or by the computer. In addition, in order to modulate the conscious experience of agency, action effects were subliminally primed by the presentation of congruent, incongruent or neutral effect stimuli prior to the action. First, we observed sensorimotor attenuation in the visual ERP selectively for self-generated action effects. That is, the N1 component, a negative deflection around 100 ms following a visual stimulus, was smaller in amplitude for visual effects caused by the subject as compared to effects caused by the computer. Second, congruent effect priming enhanced the explicit judgment of agency and further reduced the N1 amplitude for self-generated effects, even though effect primes were not consciously processed. Taken together, these results provide evidence of a top-down modulation of sensory processing of action effects by prior effect information, and support the neurophysiological mechanism of sensorimotor attenuation as underlying self-registration in action. Our findings suggest that both efferent information and prior thoughts about the action consequence provide important cues for a pre-reflective form of the experience of being an agent.

1 Introduction

How do we come to experience that we are causing our thoughts, actions and even external events? The perceptual experience of voluntary actions comprises a sense of self in action, that is, a sense of causing and controlling the action and its perceptual consequences. If we think about turning on the light and flip the switch, we will automatically and indubitably feel that we ourselves caused the light to come on and not somebody or something else. This form of self-awareness is called the sense of agency and it mostly remains pre-reflective, that is, in most actions we are not explicitly conscious of it (Gallagher, 2000). It can be disturbed in psychiatric patients, most typically in the case of schizophrenia, with delusions of control and symptoms of thought insertion. These patients interpret their own thoughts or actions as being controlled or influenced by someone else (Blakemore, Wolpert, & Frith, 2002). Despite an increasing body of research on the sense of agency (David, Newen, & Vogeley, 2008), the underlying neurocognitive mechanisms are not well understood, in part because studies have used different measures and targeted different levels of the sense of agency, meaning that findings cannot be related directly to each other.

A recent conceptual framework (Synofzik, Vosgerau, & Newen, 2008) distinguishes at least two important representational levels of the sense of agency: the feeling of agency (i.e., a sense of coherence in action processing) and the judgment of agency (i.e., a reflexive attribution of authorship), with different cues entering each level. The judgment of agency is thought to result from a higher-order reflective inference made on the basis of giving weight to cognitive indicators such as contextual cues and belief states. In contrast, the feeling of agency, being part of the “minimal” or “embodied” self (Gallagher, 2000; Jeannerod, 2007), is not based on conscious reflection but is assumed to depend on automatic processing of central and peripheral signals generated by the action itself.

Importantly, most studies so far have used explicit measures requiring reflective authorship attribution, and therefore only captured the level of judgment of agency, for example, by asking participants to indicate whether they or the computer caused a visual effect (Aarts, Custers, & Wegner, 2005). These studies neglected an important aspect of agency, namely the non-conceptual immediate feeling of one’s action, which can only be assessed by implicit measures. In fact, in our everyday lives, a non-reflective phenomenal experience is more common than an explicit representation of selfhood. Our sense sense of self persists even when we are not engaged in explicit reflection. Imagine the situation where you intend to cross a road. You will focus your attention on the coming cars but not on yourself even though you are conscious of yourself, albeit in a non-reflective manner. An implicit measure that has been proposed to capture this background experience of one's action is the attenuation of self-produced sensations (Blakemore, Wolpert, & Frith, 2000), and this was in the focus of our experiment.

Sensory attenuation has been widely investigated by psychophysical studies exploring, for instance, the basis of why individuals cannot tickle themselves (Blakemore, Frith, & Wolpert, 1999; Weiskrantz, Elliott, & Darlington, 1971). This mechanism is considered to optimize motor control but also to facilitate the ability to differentiate sensations caused by oneself from those caused by other agents or external stimuli. Recent neuroscientific research has started to specify the underlying neural processes of this. Functional neuroimaging studies, for example, report less activation of the primary somatosensory cortex for self-generated as compared to externally-generated tactile stimuli (Blakemore, Wolpert, & Frith, 1998; Helmchen, Mohr, Erdmann, Binkofski, & Buchel, 2006). Furthermore, research using electroencephalography (EEG) has shown reduced amplitudes of auditory event-related potentials (ERP) following self-produced acoustic sensory input (Curio, Neuloh, Numminen, Jousmaki, & Hari, 2000; Houde, Nagarajan, Sekihara, & Merzenich, 2002; Martikainen, Kaneko, & Hari, 2005).

Since attenuation shows up in different sensory systems, it seems to rely on a general modality-independent mechanism. It has been suggested that sensory attenuation reflects a reduction in the perceptual prediction error depending on forward-model predictions based on efference-copy (Blakemore, Wolpert, & Frith, 2000; Sperry, 1950; von Holst & Mittelstaedt, 1950). The cerebellum and parietal cortex have been shown to play a central role in the processing of prediction error (Blakemore & Sirigu, 2003; Miall, Weir, Wolpert, & Stein, 1993; Wolpert, Miall, & Kawato, 1998). Besides precise spatio-temporal predictions derived from motoric signals, however, recent studies revealed that, at higher cognitive levels, anticipation based on motor preparation (Voss, Ingram, Haggard, & Wolpert, 2006; Voss, Ingram, Wolpert, & Haggard, 2008) also contributes to this self-specific suppression effect.

Until now, existing models of the sense of agency focus exclusively either on its sensorimotor underpinnings (Blakemore, Frith, & Wolpert, 1999; Frith, Blakemore, & Wolpert, 2000) or, in contrast, on higher-level inferences which are unrelated to internal movement-related information (Wegner, 2002). Neither model, however, has yet looked at their interrelation. For example, the theory of apparent mental causation (Wegner, 2002, 2003) assigns a central role to cues that are independent of action execution such as thoughts and beliefs prior to the action or contextual information. It is assumed that these cues are used by a mental inference mechanism for generating a sense of agency. This view suggests that people think they have caused a light to turn on - even if they actually did not act at all - if they were thinking about it just before it happened and if there seem to be no alternative possible cause. Evidence supporting this theory has been provided by studies which used priming to manipulate thoughts about an action effect before the action was actually performed (Aarts, Custers, & Wegner, 2005; Linser & Goschke, 2007; Moore, Wegner, & Haggard, 2009; Sato, 2009; Wegner & Wheatley, 1999). The typical finding is that consistency between a prime and a subsequent action effect enhances the reported experience of agency even if the effect has in fact not been caused by the subject's action and is therefore independent of the motor system execution commands.

In contrast, the motor-prediction model of agency, derived from theories on motor control (Wolpert, Ghahramani, & Jordan, 1995), claims that the sense of agency depends on predictions of an internal forward model which are compared to input from sensory systems (Frith, Blakemore, & Wolpert, 2000). In particular, the forward model receives a copy of the motor command (von Holst & Mittelstaedt, 1950) that is transformed into the expected sensory consequences resulting from the particular action. It is further assumed that a comparator mechanism then matches the predicted and actual sensory outcome: Congruency induces a sense of agency whereas incongruence leads to the experience of external causation (Synofzik, Vosgerau, & Newen, 2008). That is, according to this view, the experience of having caused a light to turn on depends on the action of flipping the switch and the predictions based on the learning history of this action-effect coupling. Evidence for the comparator model has been provided by a number of behavioral and neurophysiological studies as well as patient studies (Blakemore, Wolpert, & Frith, 1998; Feinberg & Guazzelli, 1999; Ford & Mathalon, 2004; Sato & Yasuda, 2005; Shergill, Bays, Frith, & Wolpert, 2003; Voss, Ingram, Haggard, & Wolpert, 2006).

However, despite the evidence that different cues (e.g., motor-prediction and prior thoughts) can contribute to the sense of agency, their specific contribution to the different levels of agency and their integration has not been studied yet. The present study sought to address this issue by focusing on sensory attenuation as a possible neural proxy (i.e., as a non-verbal measure of the feeling of agency) and to compare it to an explicit, verbal measure capturing the judgment of agency.

The specific aim of the present study was twofold. First, our purpose was to verify whether sensory attenuation can also be identified in the visual and not only in the auditory ERP, and can be considered a possible implicit neural indicator of the sense of agency (cf. Gallagher, 2000). Second, and more importantly, we aimed to find out whether prior thoughts about the consequence of an action can not only influence the reflective experience of control (i.e., the judgment of agency) but can also modulate early sensory processing, in terms of enhancement or attenuation (i.e., the feeling of agency). For example, if one accidentally flips a light switch by leaning against a wall, the sudden illumination would probably be unexpected and one might not immediately consider oneself as being the cause. In contrast, if an individual anticipates the appearance of the light, for example due to somebody else warning him or her, the sudden light would certainly be less unexpected and attention-getting and accompanied by an immediate feeling of causation. This modulation of attention might be mediated by the process of sensory attenuation for example.

To investigate these issues, we recorded the EEG activity while participants viewed either self- or externally-generated visual effects. Critically, we used masked priming in order to establish a subliminal thought about the action effect prior to the action. It has been shown that the illusion of conscious control over an action effect even occurs under conditions in which the prime is presented below the level of conscious awareness (Aarts, Custers, & Wegner, 2005; Linser & Goschke, 2007). In particular, we were interested in how prior thoughts can affect sensory attenuation of self-generated visual effects in early ERP components such as N1. Furthermore, participants gave estimates of the causal relation between their action and the effect as a measure of the judgment of agency. Based on theories of motor-control, we expected a reduced magnitude in the N1 component as a reflection of sensory attenuation, specifically linked to self-generated effects. According to the inferential account, priming should affect the conscious judgment of agency (i.e., enhance causality estimates in cases in which prime and effect are congruent). Moreover, since the effect anticipation can be matched to the actual sensory input and thereby reduce the sensory prediction error, we predicted that a congruency between prime and subsequent effect should lead to further attenuation of the early visual ERP. In other words, we predicted that a cognitive agency indicator such as prior thoughts about a subsequent effect is integrated not only at the level of conscious judgments but already at the level of primary perceptual processing (i.e., the level of feeling of agency). Furthermore, according to the inferential account, the influence of prior thoughts is independent of efferent motor information, and therefore, the impact of priming should be present even if effects are not actively produced by a person.

2 Methods

2.1 Subjects

Twenty-four right-handed subjects (12 women; mean age 24 years, range 19-31 years), with normal or corrected to normal vision participated in the experiment after providing written informed consent. The study was performed in accordance with the declaration of Helsinki.

2.2 Task and procedure

In line with previous ERP research on sensory attenuation (Bäss, Jacobsen, & Schröger, 2008; Martikainen, Kaneko, & Hari, 2005), the experiment consisted of three different tasks (see Fig. 4.1). In the motor-effect task (ME), subjects self-generated visual action effects, whereas in the effect-only task (E), the same visual effects were externally generated. Differences in the effect-related ERP between the ME and E task would indicate self-specific processing of visual action consequences. A motor-only task (M) served as a control task to rule out motor activity as a possible confounding factor in the comparison between the ME and E task.

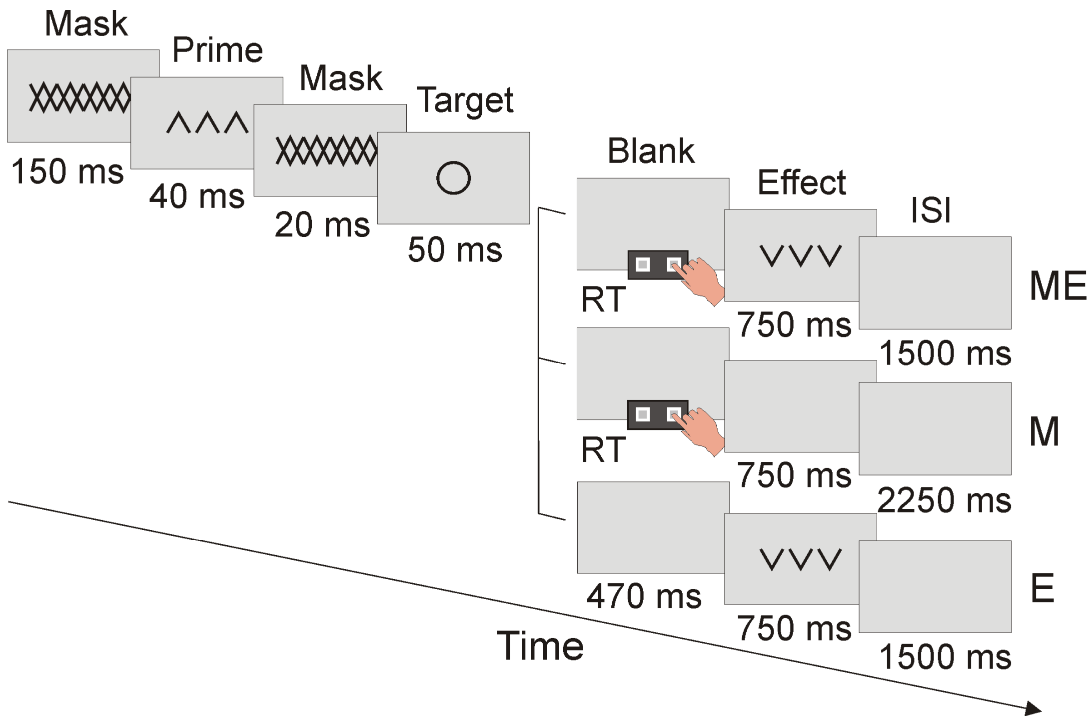

Figure 4.1. Sequence of stimulus events in the ME, E and M tasks. Trials with an incongruent prime-effect relation are shown for the ME and E tasks.

The ME task was a modified version of the agency paradigm described by Linser and Goschke (2007) in which subjects gave forced-choice left and right key press responses which triggered the appearance of one of two alleged effect stimuli. Participants were asked to pay attention to the relation between the choice of the response key and the type of effect stimulus. Stimuli were displayed in black on a gray background using Presentation software (Neurobehavioral Systems, Inc.). Each trial began with a 150 ms presentation of a forward mask, which was followed by a prime (40 ms) and a backward mask (20 ms).

The prime stimuli consisted of a set of three arrows pointing either upwards or downwards (subtending a visual angle of 0.3° x 1.6°). The mask was composed of up and downward pointing arrows superimposed on each other, subtending an angle of 0.7° x 2.3°. Following the backward mask, one of two target stimuli (a circle or square) was randomly selected, presented for 50 ms (with a visual angle of 0.5° in width and height) and replaced by a blank screen which remained until participants pressed the left or right key. The target-response mapping was counterbalanced across participants. After a 20 ms delay, responses were followed by either up or downward pointing arrows (of the size of the prime stimuli), which were presented for 750 ms and followed by an inter-stimulus-interval of 1500 ms. In order to create a context of agency ambiguity, the contingency between action and effect was lowered to 75%, a degree at which the influence of effect priming has been demonstrated in previous studies (Linser & Goschke, 2007; Sato, 2009). That is, the mapping of the target stimulus, which determined the action choice, and the effect stimulus was not consistent across all trials: In 75 % of the trials, one particular target stimulus was related to one particular effect stimulus, whereas in the remaining 25 % of trials, the opposite mapping appeared. This target-effect mapping was counterbalanced across participants.

After each block of 48 trials, the experience of control was assessed using a 10 cm visual analog scale (VAS). Subjects had to judge the degree to which they thought that their key press (left or right) determined the pointing direction of the arrows on a scale ranging from 0% (no control) to 100% (full control). The critical factor was the relationship between prime and effect stimuli, which was either congruent (arrows pointed in the same direction), incongruent (arrows pointed in the opposite direction) or neutral (primes consisted of superimposed up and downward arrows). The prime-effect relation was varied blockwise and participants performed 3 blocks of 48 trials for each prime-effect condition.

The E task was an observation task in which stimuli were externally generated by the computer with identical timing as in the ME task. That is, subjects just passively viewed the same visual scenario. In place of the response window and the button press, a blank screen appeared for a duration of 470 ms, which was selected to mirror the mean reaction time in the ME task. The subsequent effect stimuli were presented with the same target-effect mapping (75/25) as in the ME task. Participants were again asked to pay attention to the causal relation between the target stimulus and the subsequent effect stimulus and had to judge the degree to which the target determined the pointing direction of the arrows on a VAS ranging from 0 to 100 as in the ME task. The prime-effect relation was varied blockwise, as in the ME task, and participants performed 3 blocks of 48 trials for each condition.

In the motor-only task (M), subjects had to respond to the target stimuli in the same manner as in the ME task, but no visual effect stimuli were presented. That is, responses were followed by a blank screen for 2250 ms until the next trial started. The order of the tasks was fixed across all participants: Six alternating blocks of ME and E tasks were followed by one block of the M task consisting of 48 trials and a two minute break (ME-E-ME-E-ME-E-M-break). This sequence of tasks was repeated three times.

2.3 Prime awareness and prime processing

After the main experiment, participants performed two additional control tasks which aimed to test whether prime stimuli were perceived even though subjects were unaware of them. First, subjects performed a response priming task which was used to measure prime perception. Subjects pressed the left or right key as quickly and as accurately as possible in response to one of two target stimuli. Stimulus material was the same as in the ME task except that the former effect stimuli served as targets (up or downward pointing arrows), and responses were no longer followed by an effect. The interstimulus interval was 1500 ms. The relation between prime and target stimulus was either congruent, incongruent or neutral. Differences in reaction times between any of these conditions would indicate that prime stimuli were perceived. The target-response mapping was counterbalanced across participants. Twelve practice trials were followed by a random sequence of 180 trials with 60 trials per condition.

Furthermore, at the end of the experiment, prime awareness was assessed using self-report (in a structured interview) as a subjective measure and a prime-discrimination task as an objective measure. The latter task consisted of the same stimulus material as the ME task except that targets were now replaced by a question mark (50 ms duration, 0.5° x 0.5°). Subjects were instructed to attend to the masked prime stimuli and to try to discriminate between them by pressing the left button for upward pointing arrows and the right button for downward pointing arrows, and to guess if they did not recognize the pointing direction. The prime-response mapping was the same as in the target-discrimination task. Primes appeared in random order and 160 trials were presented.

2.4 EEG recording and analysis

The electroencephalogram (EEG) was recorded from 64 scalp Ag-AgCl electrodes embedded in a fabric cap according to the international 10-20 system (BioSemi Active II system, BioSemi, Amsterdam, Netherlands). The electro-oculogram (EOG) was recorded from electrodes placed external to the outer canthus of each eye and below and above the right eye.

All channels were referenced to the left mastoid and signals were amplified and digitized at 512 Hz.

Analysis of EEG data was performed using Brain Vision software (Brain Products GmbH, Gilching, Germany). EEG recordings were low-pass filtered at 30 Hz, high-pass filter at 0.75 Hz and re-referenced to average reference. Non-stereotyped muscular artifacts such as swallowing or temporary electrode artifacts were identified by visual inspection and rejected from further analysis. Repeatedly occurring, stereotyped artifacts such as eye movements or heartbeat were identified and removed using independent component analysis (ICA) (Jung et al., 2000). This procedure led to a rejection of 1.4% of epochs on average (mean: 13.97, range: 2-38). Two participants were excluded from the ERP analysis because of excessive movement-related artifacts. Subsequently, stimulus-locked data epochs were computed (-200 to 400 ms) and baseline-corrected using a 100 ms window before the response. Separate ERP average waveforms were then computed for each of the three tasks (ME, E, and M task) and for each of the three prime-effect conditions (congruent, incongruent, and neutral, separately for the ME and E task). Finally, grand mean ERPs were calculated by averaging each condition across participants. Only trials with correct responses (mean percentage: 99 %) were included in grand mean average ERPs and statistical analyses.

Sensory attenuation effects in the auditory modality have been found to be most prominent around 100 ms following the effect stimulus over fronto-central brain regions (Bäss, Jacobsen, & Schröger, 2008; Martikainen, Kaneko, & Hari, 2005). The visual N1 has distinct subcomponents (Vogel & Luck, 2000), an early anterior subcomponent peaking around 100 ms after stimulus onset over fronto-central sites and a late posterior subcomponent peaking around 160 ms after stimulus onset over inferoposterior sites. In our analysis, we focused on the anterior N1 component and quantified its mean amplitude in the average ERP waveform of each experimental condition for each participant at nine electrode sites in the fronto-centro-parietal region (FC3, FCz, FC4, C3, Cz, C4, CP3, CPz, CP4). Mean voltages were calculated in the 80 to 130 ms time interval following the onset of the effect stimuli. The measurement window comprises the latency of the anterior visual N1 component usually reported in the literature (Vogel & Luck, 2000). The impact of a possible oddball effect in the N1 time range was examined and excluded. Since no difference in N1 amplitude was observed for standard and deviant effect stimuli, both standards and deviants were included in the average ERP to increase the signal-to-noise ratio.

2.5 Statistical analysis

Mean ERP voltages were submitted to a four-way repeated-measure analysis of variance (ANOVA) with the factors task (2 levels: ME, E), prime-effect condition (3 levels: congruent, incongruent, neutral), anterior-posterior electrode location (3 levels: FC, C, CP) and lateral scalp location (3 levels: 3=left; z=midline; 4=right). If data violated the sphericity assumption, we applied the Greenhouse-Geisser correction. We used Tukey's HSD test as a multiple comparison post-hoc procedure for further examination of differences and interactions between task, priming condition and electrode location. All measured amplitude values were tested for normal distribution with the Kolmogorov-Smirnov test.

3 Results

3.1 Behavioral results

In the prime discrimination task, subjects' ability to discriminate prime stimuli was at chance level (one-sample t-test with the chance level of performance set at 50%, $t(19) = 1.14$, $p = 0.27$), which indicates that subjects were not aware of the prime stimuli. Two participants who reported conscious prime detection were excluded and further analyses were conducted with data from the remaining 20 subjects.

In the response priming task, we observed significant differences in reaction times, $F(2,38) = 53.01$, $p < .001$, and error rates, $F(2,38) = 9{,}04$, $p < .001$, depending on prime-effect congruency. This indicates that, despite being unaware of the stimuli, participants' perception was influenced by the prime stimuli. Reaction times were faster in congruent trials (*M*=403 ms, *SEM*=49.72) as compared to incongruent trials (*M*=452 ms, *SEM*=44.39), $p < .001$, or neutral trials (*M*=420 ms, *SEM*=49.31), $p < .01$, and the error rate was lower for congruent trials (*M*=4.4%, *SEM*=3.19) as compared to incongruent trials (*M*=10.6%, *SEM*=7.02), $p < .001$. Figure 4.2 displays mean explicit agency judgments for different prime-effect conditions and separately for the ME and E task.

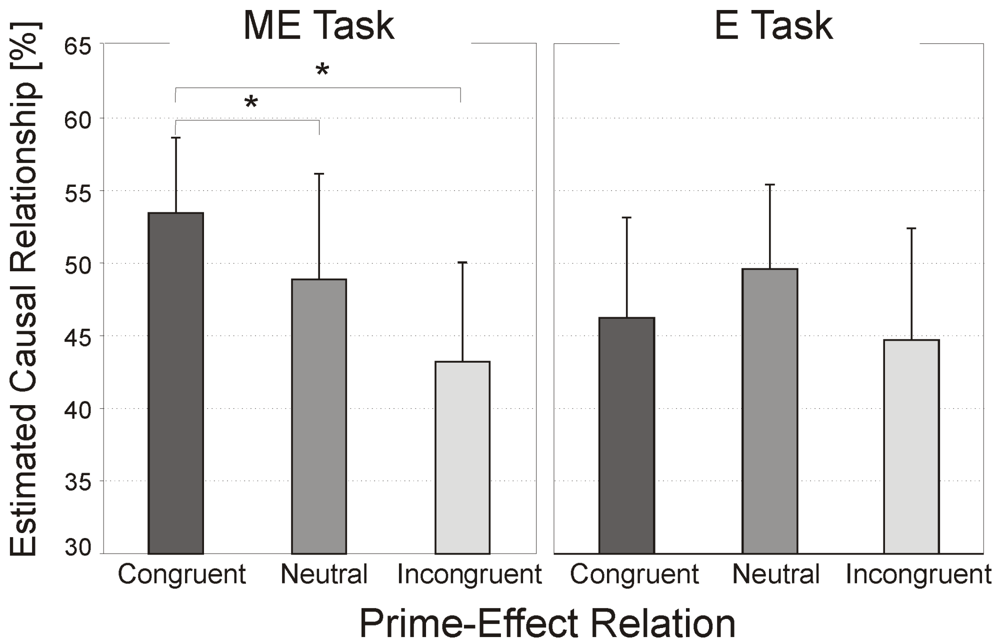

Figure 4.2. Mean control judgments in the ME task and the E task as a function of prime-effect congruency. Error bars represent 95% confidence intervals.

The ANOVA with mean rating scores given in the ME task as the dependent variable yielded a significant main effect of prime-effect congruency, $F(2,38) = 4.32$, $p < .05$. A Tukey HSD post-hoc test revealed that participants reported a significantly stronger experience of control over the effect stimuli after blocks with congruent (*M*=53.5, *SEM*=2.48) as compared to incongruent prime-effect pairs (*M*=43.2, *SEM*=3.26), $p < .05$. No significant difference in control judgments was found between congruent and neutral trials (*M*=48.9, *SEM*=3.49, $p > .15$), or incongruent and neutral trials ($p > .15$). The prime-effect conditions were not associated with differences in mean reaction times ($p > .15$) or error rates ($p > .15$); hence, response differences cannot account for the effect on perceived control.

In the E task, participants also provided causality judgments concerning the relation between target stimuli and effect stimuli. This judgment task was included in order to ensure comparable levels of involvement and attention between both the ME and E tasks. In contrast to results obtained in the ME task, the ANOVA for the E task showed no significant difference in causality judgments between conditions of congruent (*M*=46.3, *SEM*=3.31), incongruent (*M*=44.8, *SEM*=3.67) and neutral priming (*M*=49.6, *SEM*=2.80, $p > .15$).

3.2 ERP results

Anterior N1 Scalp Distribution

Figure 4.3A displays the grand-average ERP waveforms recorded at fronto-central, central and centro-parietal electrodes obtained during the E and ME task, separately for the three experimental prime-effect conditions. In Figure 4.3B, the scalp map of the difference wave between the E task and ME task is shown. An anterior N1 component is evident in the ERP waveform as a negative deflection peaking around 100 ms after stimulus onset, with a mid-central scalp distribution.

The ANOVA across both tasks revealed a main effect of anterior-posterior electrode location, $F(2,38) = 15.52$, $p < .001$, which indicated that N1 was larger over fronto-central and central compared to centro-parietal brain regions. A significant interaction between laterality and anterior-posterior electrode location was present, $F(2,38) = 4.74$, $p < .01$. This interaction effect showed that at central and centro-parietal sites, the N1 amplitude was larger at midline than at lateral electrodes, all *ps* < .05, whereas at frontal sites, no difference between midline and lateral electrodes was present. Comparisons between left versus right hemisphere electrode positions did not reveal significant differences in N1 amplitudes. No differences in scalp distribution of the ERP were observed between the ME and E task.

Anterior N1 and Sensory Attenuation

From Figure 4.3A, it is clear that the N1 wave is larger for effect stimuli elicited in the E task than in the ME task. However, prior to computing and comparing N1 amplitudes, we first had to correct for component overlap in the ME task. In our task design, stimulus and response occurred simultaneously in the ME task, such that brain responses elicited by stimulus processing and motor activity were likely to overlap and distort the computed stimulus-locked ERP waveforms. The corrected ERPs in the ME task were obtained by subtraction of activity elicited by the M task in which only motor responses and no effect stimuli occurred. Figure 4.3C demonstrates that motor-related activity did not modulate the N1 amplitude. By using the corrected ERPs in all subsequent analyses, the influence of motor activity as a confounding factor in the observed differences between the tasks could be ruled out.

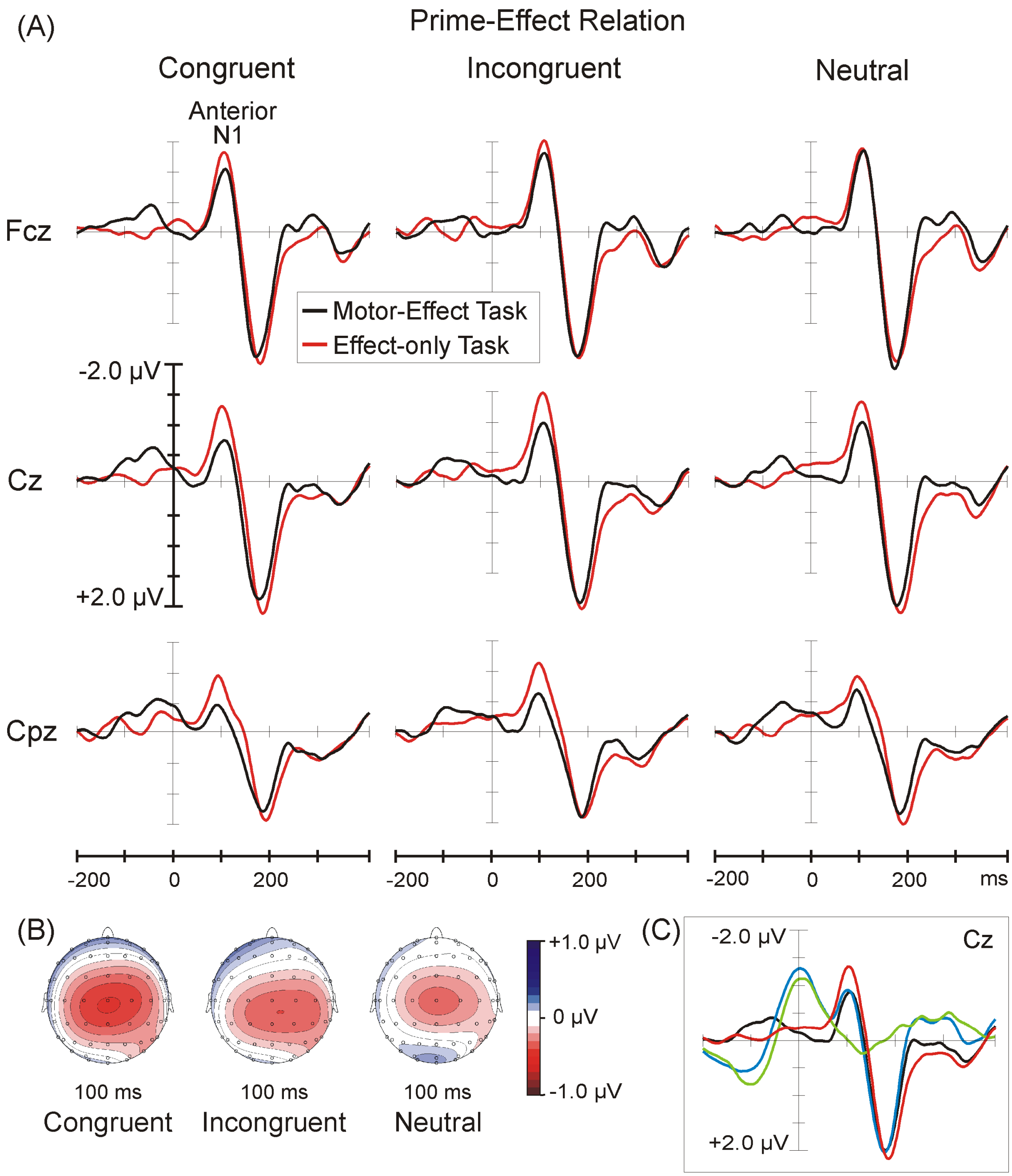

Figure 4.3. (A), Stimulus-locked grand-average ERP waveforms for the E and ME tasks at electrodes FCz, Cz and CPz and, (B), scalp topographies of the voltage difference between E and ME tasks, separately for the three priming conditions. (C), Grand-average ERPs for the E task (red), ME task (blue), M task (green) and ME minus M task (black) for the vertex electrode (Cz). Negativity is plotted upwards.

Anterior N1 and Effect Priming

Results of an ANOVA across tasks and electrode sites showed a main effect of prime-effect congruency, $F(2,38) = 5.02$, $p < .05$, indicating smaller amplitudes for congruent prime-effect conditions as compared to incongruent and neutral priming. Priming and laterality interacted significantly, $F(4,76) = 4.03$, $p < .01$, due to a larger effect of priming at midline compared to lateral electrodes. The interaction between prime-effect congruency and task did not reach significance, $F(2,38) = 2.34$, $p = .10$.

In order to further investigate the differential effects of priming on N1 amplitudes, we computed separate ANOVAs for the ME task and the E task, including the factors prime-effect condition, anterior-posterior electrode location and laterality. Figure 4.4 shows grand-average ERP waveforms for the ME task and the E task at electrode Cz as a function of priming.

In the ME task, there was a significant main effect of prime-effect congruency on N1 amplitude, $F(2,38) = 6.87$, $p < .01$, indicating smaller amplitudes for congruent effect priming as compared to incongruent and neutral effect priming. Focusing on electrode site Cz, we conducted Tukey's HSD post-hoc comparisons of amplitudes between priming conditions. These analyses demonstrated that N1 amplitudes were significantly smaller for the congruent priming condition as compared to incongruent or neutral effect priming, all *ps* $< .05$, without any significant difference between the latter two conditions ($p > .15$). Moreover, we observed a significant interaction between priming and laterality, $F(4,76) = 2.86$, $p < .05$, indicating that the effect of priming was largest at midline electrodes compared to lateral sites.

For the E task, the ANOVA yielded no significant effect of prime-effect congruency on N1 amplitude and no interaction effects between priming and electrode position (*ps* $> .15$).

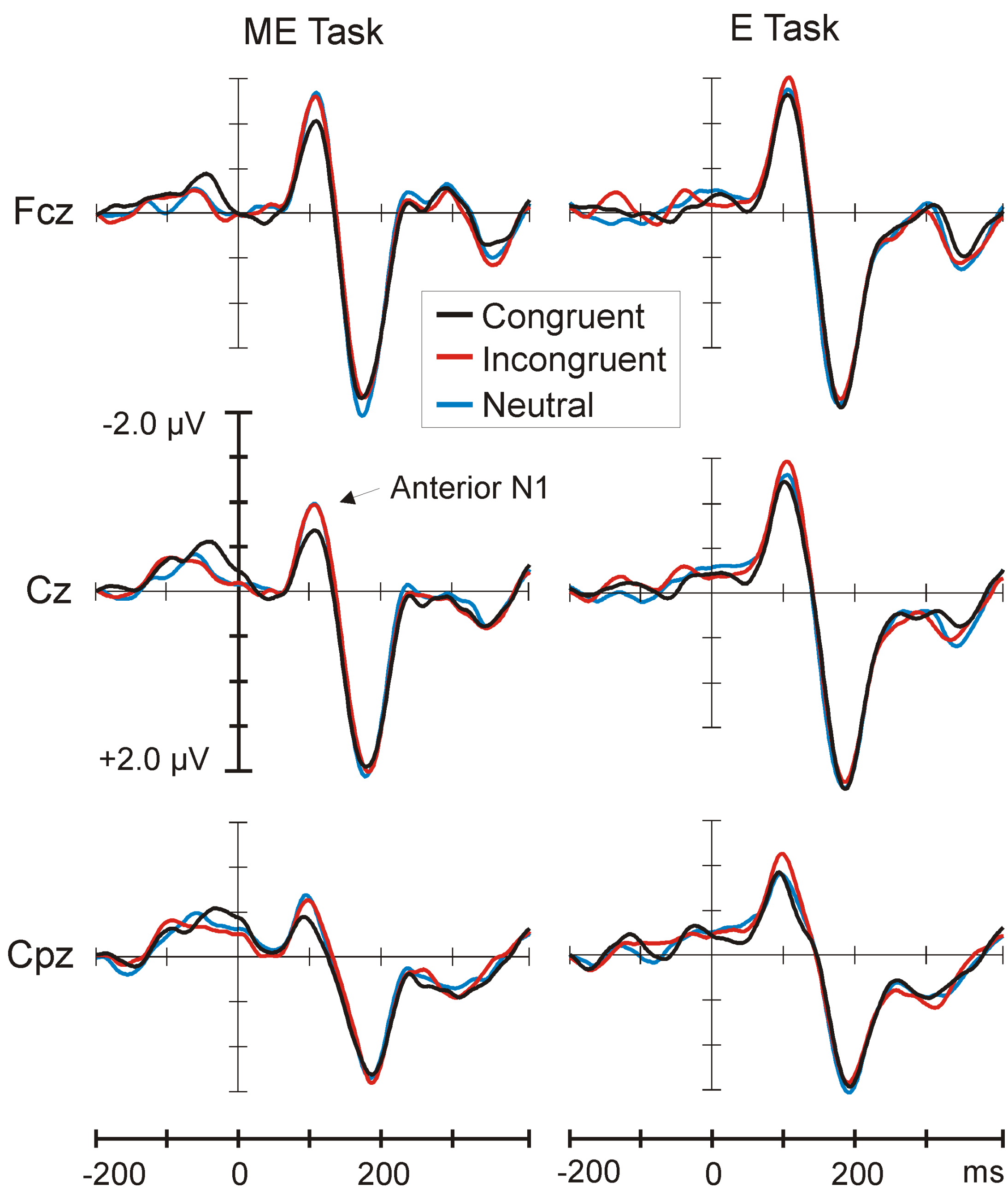

Figure 4.4. Stimulus-locked grand average ERP waveforms at FCz, Cz and CPz for the ME and E tasks as a function of prime-effect relation.

Thus far, our results demonstrate attenuation of ERP responses specifically to self-generated visual effects in the ME task. Further analyses showed that priming modulated the ERP response in the ME but not in the E task, and most strongly at central electrode locations. In order to test whether priming had an impact on the self-specific attenuation effect, we computed an ANOVA with amplitudes of the difference waves between the ME and E task. The main effect of priming did not, however, reach significance ($p = .10$) possibly due to low statistical power. Furthermore, no interaction effects between prime-effect condition and anterior-posterior electrode position or laterality were observed ($ps > .15$).

4 Discussion

4.1 Self-specific attenuation of visual effects: a sensorimotor mechanism underlying the sense of agency

The present study aimed to measure sensory attenuation in the visual event-related potential as a sensorimotor and pre-reflective marker capturing the feeling of agency. The experiment focused on the N1 wave of the visual ERP. We found the N1 component to be smaller in response to visual effects that were caused by the subjects' actions as compared to the same effects that were externally caused and passively observed by the subjects. Thus, our results indicate specific sensory attenuation in processing of self-generated visual events. In humans, sensory attenuation has mainly been shown in the auditory but also in the tactile modality, both at the subjective perceptual level (Blakemore, Frith, & Wolpert, 1999; Sato, 2009), and also at the neurophysiological level (Bäss, Jacobsen, & Schröger, 2008; Curio, Neuloh, Numminen, Jousmaki, & Hari, 2000; Houde, Nagarajan, Sekihara, & Merzenich, 2002; Martikainen, Kaneko, & Hari, 2005). This is the first ERP study characterizing the time course of sensory attenuation in the visual modality using the advantage of the high temporal resolution of EEG.

It is important to note that the N1 component cannot be compared directly across modalities, since amplitude, latency and topography differ as a function of the stimulus modality that is addressed during a given experimental protocol. In the auditory domain, for example, stimuli usually elicit larger N1 amplitudes with shorter latency than in the visual domain, in which the N1 component can be further subdivided into at least two distinct subcomponents (Vogel & Luck, 2000). Hence, task-dependent (self, other) modulation of the visual N1 amplitude is likely to be smaller than in studies using auditory stimuli. Indeed, in our experiment, the effect on the visual N1 amplitude was less pronounced than the suppression effects reported in the literature measuring the auditory N1 (Bäss, Jacobsen, & Schröger, 2008; Ford & Mathalon, 2004; Heinks-Maldonado, Mathalon, Gray, & Ford, 2005). Future studies are needed which directly compare attenuation effects across modalities.

According to theories of motor control, the availability of efferent information in the case of self-generated effects allows a forward model to make precise predictions about the upcoming action effect (Wolpert, Ghahramani, & Jordan, 1995): A match between the predicted and actual effect leads to a cancellation of the afferent information (Blakemore, Frith, & Wolpert, 1999). In contrast, no efferent information is available when the effect is externally generated. Hence, predictability of the effect is less precise and cannot be used for cancellation. These predictive processes enable the brain to already differentiate between external effects that the organism causes and those it does not cause at an early stage in sensory processing. Our study suggests that sensory attenuation is not only a mechanism to optimize motor control but that it also contributes to action perception, specifically to the attribution of action and thus the experience of agency.

It has been shown that the magnitude of the visual N1 component increases when attention is directed to the location of a stimulus, which suggests that spatial attention leads to selective amplification of sensory information flow in visual pathways (Hillyard, Vogel, & Luck, 1998; Mangun, 1995). In our study, we compared brain responses to identical visual events that were either passively observed or actively produced. It may be argued that differences in attentional processes between experimental conditions in terms of a higher level of general attention in the active response task (ME task) caused the modulation of N1 amplitudes. However, if this were the case, one would expect a N1 attenuation effect in the opposite direction, that is, an increased N1 component in the response task as compared to the observation condition (E task). In order to keep the degree of task and attentional involvement at a similar level, the subjects were required to perform causality judgments in both tasks. Thus, they directed their attention to the effect stimuli in either case by judging the causal relation between the effect stimulus and the preceding target or response, respectively. Since responses were always determined by the target stimulus, similar cognitive operations were involved in both judgment tasks. Furthermore, in a post-experiment questionnaire, subjects indicated that they did not perceive a difference in task difficulty between both conditions.

Nevertheless, even though task involvement was comparable, it could be suggested that the mere presence of an action influenced the amount of attention available for the subsequent visual event, thereby leading to a N1 reduction, independent of any predictive mechanism. We do not believe, however, that our finding of self-specific N1 attenuation is simply due to a non-specific reduction in attention because our second experimental manipulation concerning priming demonstrates that attenuation can arise from top-down expectations not associated with motor preparation and execution as indicated by the significant main effect of prime-effect congruency. Taken together, this early perceptual discrimination of the self from the non-self as reflected in N1 attenuation to self-generated effects obviously informs a basic action representation, which provides the basis for the attribution of events to our own actions (i.e., the experience of agency).

4.2 Prior effect representations contribute to the judgment of agency

The judgment of agency has been assumed to depend on effect anticipations and their respective consistency with the actual effect (cf. Wegner, 2002). In support of this, we found that agency judgments were enhanced when a prime stimulus prior to the action and the action effect were congruent as compared to when they were incongruent or unrelated, which is consistent with previous studies (Aarts, Custers, & Wegner, 2005; Linser & Goschke, 2007; Sato, 2009). We further showed that this modulation of the sense of agency occurred even though prior effect information remained at an unconscious level and the action of the subject was predetermined. These findings suggest that processes underlying the experience of agency do not necessarily become conscious. Environmental cues can be used to establish a sense of agency without entering our conscious awareness.

It seems counterintuitive that subjects experienced a sense of agency in a situation in which they could not freely chose the action. Importantly, we here investigated the agency experience for external events (and not for actions per se), which should not depend on the degree of freedom of actions and choice. For example, if a sound occurs after one is forced to press the light switch, the fact that the action was not chosen by oneself has no informative value concerning the causal relation between the button press and the sound. On the other hand, it has been argued that the formation of action-effect associations (i.e., ideomotor learning) can occur only in the case of voluntary actions (Herwig, Prinz, & Waszak, 2007), with diverging findings however (Elsner & Hommel, 2004). In line with the ideomotor principle, in the response priming task, which served as our control task, we showed that the former action effects which served as target stimuli influenced both speed and accuracy of action selection despite the fact that actions were previously exogenously driven. Moreover, as Wegner and colleagues demonstrated, priming of action effects induces a sense of agency even in the absence of an action or in situations in which the event is completely uncontrollable (Wegner, Sparrow, & Winerman, 2004; Wegner & Wheatley, 1999). That is, action effect primes can mimic voluntary actions in that they activate a representation of the action consequence prior to the action which can then be used to infer agency.

Our results further show that priming did not influence the perception of causality between two external sensory events which were unrelated to any action in a passive observation task. Interestingly, the sensory input and the actual causal relation did not differ between the active response (ME) task and the observation (E) task: In both tasks, the effect stimuli were determined to the same degree (75%) by the preceding target stimuli. The two tasks differed only in terms of whether the appearance of the effect stimulus depended on an action at all or was externally controlled by the computer. Indeed, some subjects even directly focused on the relationship between effect and preceding target in the response task, as they were aware of the fact that responses could not be chosen freely but were determined by the target. Despite these similarities between both tasks, our findings indicate that unconscious representations of upcoming external effects only then influence causality judgments when the effects are produced by an action. That is, although it has been argued that an individual's prior thoughts can also induce feelings of agency for effects generated by others even when the individual was not active (Wegner, Sparrow, & Winerman, 2004), this does not seem to be transferable to the perception of causality for events in which no actor is involved at all.

The perception of causality in general relies upon observation of spatio-temporal correlations between at least two events in order to ascribe cause and effect. Agency, as a special case of causality, implies there is an actor, namely the perceiving subject him or herself, as the cause of an external event. In order to ascribe cause and effect in the case of agency, the subject's action itself is the focus of evaluation and has to be related to the observed effect in terms of spatio-temporal correlations. Prior representations of upcoming action effects are essential for action selection, on the one hand, but also for action monitoring, on the other, by enabling a comparison between the goal of the action and the actual action effect. It is thought that priming influences these prior representations of action consequences (Aarts, Custers, & Wegner, 2005), and thereby modulates the outcome of the action-effect evaluation. In contrast, the content of prior effect representations has not been assigned a central role in the context of perceived causality between external events.

4.3 Prior effect representations modulate the feeling of agency

Prior effect representations are anticipatory or intentional states which serve as cognitive cues to the judgment of agency. However, their impact on the sensorimotor level of feeling of agency is still unknown. We expected that, analogous to the impact of efference-based predictions, prime-induced effect anticipations would also influence the N1 amplitude. Indeed, our results showed that the N1 amplitude following self-generated action effects was modulated by the congruency between prime and effect. We observed reduced N1 amplitudes when the relation between prime and effect was congruent as compared to an incongruent or neutral prime stimulus. These findings are generally in line with a previous neuroimaging study investigating the effect of unconscious semantic priming on brain responses to subsequent visible target words (Dehaene et al., 2001). This study reported reduced brain activation to target stimuli in extrastriate, fusiform and precentral regions depending on the congruency between unconscious prime stimuli and target stimuli.

Furthermore, it has been demonstrated that this stimulus-specific repetition suppression phenomenon is the consequence of top-down expectations rather than automatic bottom-up perceptual repetition effects (Summerfield, Trittschuh, Monti, Mesulam, & Egner, 2008). Thus, our results indicate that effect anticipation as an important cognitive agency indicator at the level of explicit agency judgments also serves as a cue for the sensorimotor representation of agency (i.e., the feeling of agency). It is important to note, however, that there was no significant impact of priming on the N1 amplitude difference between self and externally generated action effects even though priming exclusively affected the N1 amplitude following self-generated effects but not the N1 following externally generated effects. The lack of a statistically significant influence is probably due to low statistical power, which increases the possibility of a type II error. Alternatively, prior information (induced by priming) might possibly also have a general effect on the processing of sensory events regardless of the source of the event. However, this might have been too weak to manifest itself statistically in the context of the present experimental paradigm.

Further studies are needed which extend the present paradigm to other sensory modalities. Studies that investigated sensory attenuation in the auditory modality, for example, have reported larger and obviously more robust effects (Bäss, Jacobsen, & Schröger, 2008; Ford & Mathalon, 2004; Heinks-Maldonado, Mathalon, Gray, & Ford, 2005; Martikainen, Kaneko, & Hari, 2005). On the other hand, effect anticipation induced by priming is only one of many different agency cues that are combined to form a robust agency representation. Hence, despite the obvious impact on measures of agency, its influence is limited and complemented by other factors such as proprioceptive and motor signals as well as contextual cues and self-concept. According to recent views (Synofzik, Vosgerau, & Lindner, 2009; Synofzik, Vosgerau, & Newen, 2008), the sense of agency depends on an optimal integration and combination of a wide variety of internal and external cues at different representational levels.

Our study supports this perspective and demonstrates a new approach to the sense of agency by targeting different levels of agency processing within one experimental paradigm using implicit and explicit measures at the same time. However, the interaction of the mechanisms underlying these implicit and explicit measures (i.e., the relation between pre-reflective and reflective aspects of the sense of agency) still needs to be explored. Based on observed dissociations between action awareness and automatic action control, it has, for instance, even been argued that the conscious experience of action cannot depend on endogenous signals used for motor control since they are poorly accessible to consciousness (Fourneret & Jeannerod, 1998; Georgieff & Jeannerod, 1998). However, in the present study, we demonstrated that subliminal information about an action outcome can have an impact not only on the conscious experience of action but also on automatic, unconscious processes of motor control and sensory gating. In order to do justice to the complex phenomenology of agency, future studies are needed to further explore the relative weighting by which different conscious and unconscious cognitive, sensory and motor-related signals are integrated at different perceptual stages.

In conclusion, we here show that both subliminal effect anticipation induced by priming and efference-based prediction seem to have similar effects at early stages of sensory processing of an action consequence. Whereas the comparator and inference models emphasize distinct agency indicators, with these being motor-related information and prior thoughts, respectively, both seem to influence the sense of agency not only at the level of conscious judgments but also at the level of non-conceptual feeling. That is, the comparator mechanism which matches expected and actual action consequences can be fed by different agency cues derived from internal or external sources, and the outcome of this comparison is already reflected at the level of immediate perceptual processing. The resulting attenuation of brain responses to sensory input in the case of agreement between expectation and actual state is accompanied by a feeling of action completion and control, and thereby contributes to the conscious experience of being the agent.

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5 Manuscript of Study 2

Reliability of sensory predictions determines the experience of self-agency

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Abstract

This study examines the neurocognitive mechanisms underlying the sense of agency, that is, the experience of causing and controlling events in our environment. Specifically, we tested the hypothesis that the sense of agency depends on an optimal integration of different anticipatory signals, generated by motor and nonmotor systems. An established marker of pre-reflective agency experience is the suppression of neural responses to actively generated feedback as compared to passively observed feedback, which was measured here by event-related potentials (ERPs). Sensory expectations based on motor-related and unrelated signals were induced by varying the probabilistic contingency between action and feedback, and by priming the feedback prior to the action. Moreover, simultaneous conscious agency judgments were assessed. Suppression of the N1 component of the ERP was found specifically to self-generated feedback, and was further affected by accurate anticipations based on prime stimuli, independent of the precision of motor predictions. Conscious agency judgments, in contrast, were enhanced by prime stimuli only in situations where no precise motor predictions of the action feedback were available. These results indicate that anticipatory signals arising from motor and nonmotor systems are integrated differently depending on the level of agency processing. Our findings suggest that, at a pre-reflective level, the brain's agency system relies on both embodied signals and nonmotor sensory expectations. At higher cognitive levels, motor and nonmotor cues are weighted differently depending on their relative reliability in a given context, thereby providing a basis for robust agentive self-awareness.

Keywords

Sense of agency, Sensory suppression, Motor prediction, Forward model, ERP, N1

1 Introduction

The experience of being the cause of one's actions and controlling sensory events in the environment serves as a key motivational force for human behavior. The term agency refers to the capacity for instrumental action, which is based upon the ability to perceive dependencies between actions and their consequences. An important source of signals contributing to this form of self awareness is foreknowledge or predictive processing of the sensory consequence that follows an action (Heinks-Maldonado et al., 2007; Michotte, 1963; Wegner, Sparrow, & Winerman, 2004). Pathological disruption of the sense of agency has been associated with deficits in internal prediction mechanisms, for example, in the case of schizophrenic patients with delusions of control, i.e., misattribution of actions to external causes (Frith, 2005).

Internal sensory predictions, that is, internal models of future bodily states or environmental events following an action, can be generated by the motor system (Wolpert & Miall, 1996). In addition, sensory predictions can also arise from various other systems which take the current context, previous perceptual experiences and other predictive cues into account (for review, see Bubic, von Cramon, & Schubotz, 2010; Summerfield et al., 2006). Research on the neurocognitive basis of the sense of agency has focused mainly on sensory predictions of the motor system. Several studies have demonstrated that explicit agency judgments strongly depend on the comparison between a sensory expectation derived from efferent information and the actual sensory feedback following the self-generated movement (Blakemore, Wolpert, & Frith, 2000; Blakemore, Wolpert, & Frith, 2002; Sato & Yasuda, 2005). It has been suggested that the experience of agency for the sensory event emerges in cases where the action outcome matches the initial expectation.

Another line of research, in contrast, ascribes a crucial role to expectations arising independent of the operation of the motor system (Wegner, 2002; Wegner & Wheatley, 1999). For example, it has been shown that inducing a representation of the sensory consequence prior to the action by means of priming enhances the conscious experience of agency (Aarts, Custers, & Wegner, 2005), even if efferent signals are absent (Wegner, Sparrow, & Winerman, 2004). Furthermore, this effect is present for supraliminal as well as subliminal primes, that is, no matter whether the prime stimulus is conscious or not (Linser & Goschke, 2007; Moore, Wegner, & Haggard, 2009).

These proposed agency cues arising from different systems are not mutually exclusive, however. A current theoretical framework suggests that the brain's agency system combines and integrates different cues depending on their relative reliabilities in certain contexts and depending on the level of agency registration (Synofzik, Vosgerau, & Lindner, 2009; Synofzik, Vosgerau, & Newen, 2008). The present study aimed to test this hypothesis of optimal cue integration by comparing the impact of different types of sensory predictions at two levels of agency registration, at the implicit, sensorimotor level, and the explicit, higher-order cognitive judgment level. It is important to note that most studies exclusively focus on higher cognitive levels of agency processing by measuring explicit judgments of agency only. This, however, does not do justice to the complex phenomenology of agency and to the fact that in our everyday lives, a non-reflective experience is more common than an explicit representation of selfhood. At least two different levels of agency representation can be distinguished, a reflective and a pre-reflective level, and it has been proposed that different cognitive cues are combined to establish one or the other representation (Synofzik, Vosgerau, & Newen, 2008). A measure that has been used to quantify the pre-reflective level of agency is self-specific sensory suppression, which refers to the fact that the sensory intensity of self-generated events is lower than for external events (Bulot, Thomas, & Delevoye-Turrell, 2007; Sato, 2009; Synofzik, Vosgerau, & Newen, 2008).

Sensory suppression is reflected for instance in the phenomenon that you cannot tickle yourself since self-produced tactile sensations are perceived as less intense as compared to the same sensations produced externally (Bays, Wolpert, & Flanagan, 2005; Blakemore, Frith, & Wolpert, 1999; Shergill, Bays, Frith, & Wolpert, 2003; Weiskrantz, Elliott, & Darlington, 1971). Neuroimaging studies have found suppressed neural activity in sensory areas specifically in response to self-generated sensory input (Blakemore, Wolpert, & Frith, 1998; Chapman, 1994; Curio, Neuloh, Numminen, Jousmaki, & Hari, 2000). Moreover, the N1 component of the event-related potential (ERP) has been proven to reflect an early indicator of this self-specific sensory gating. In fact, there are a number of studies showing a reduction in N1 amplitude when a sound is self-generated as compared to when it is externally generated (Curio, Neuloh, Numminen, Jousmaki, & Hari, 2000; Ford et al., 2001; Houde, Nagarajan, Sekihara, & Merzenich, 2002; Martikainen, Kaneko, & Hari, 2005). Similarly, the visual N1 has also been found to be sensitive to the distinction between self-causality versus external causality (Gentsch & Schütz-Bosbach, in press; Schafer & Marcus, 1973).

The explanation of sensory suppression is based on the idea of forward models of motor control generating predictions of the sensory consequences of a motor command, which are compared to the actual sensory feedback and removed in case of a match (Blakemore, Frith, & Wolpert, 1999; von Holst & Mittelstaedt, 1950). This predictive mechanism serves to signal unexpected changes in the environment. It can further be used to distinguish self- from externally generated sensations, and therefore serves as an indicator of the sense of agency, in particular, at the pre-reflective level of agency. However, the precise nature of the predictions used to gate afferent sensory information with regard to the spatial, temporal and qualitative characteristics of the sensory event are still not clear (Tsakiris & Haggard, 2003).

The present study investigated how sensory predictions from different cognitive systems are integrated by the agency system depending on the specificity and reliability of each source of information. We measured N1 attenuation in the visual ERP to self-generated stimuli, as a marker for pre-reflective agency registration, as well as assessing the participants' explicit perception of causality for those stimuli at the reflective level of agency experience. The mere presence of motor-related predictions was manipulated by having subjects generate a visual stimulus by key press as compared to passive observation of the same sensory event. In addition, the contingency between a specific type of action and a specific type of visual consequence was varied between high (75%) or low (50%) contingency so as to create contexts in which highly specific and precise motor-related predictions were available or not. Furthermore, sensory expectations independent of the motor system were induced by priming the visual action consequence prior to the action.

According to the hypothesis of optimal cue integration (Synofzik, Vosgerau, & Newen, 2008), the agency system should apply higher weight to the more reliable information sources. Therefore, we predicted that prime-induced expectation of the action consequence should enhance the sense of agency more strongly if no precise motor-related predictions are available. Furthermore, the nature of motor predictions underlying sensory suppression, that is, the precision, timescales and types of those predictions, is still under debate. While some studies have demonstrated that temporal proximity (Bays, Wolpert, & Flanagan, 2005; Blakemore, Frith, & Wolpert, 1999) and precise spatial predictions (Blakemore, Frith, &

Wolpert, 1999) are important, other suggest that the mere presence of embodied (i.e., motor-related) signals is sufficient, and proximity of the sensory event or precision of sensory predictions does not matter (Lange, 2011; Tsakiris & Haggard, 2003). Hence, if sensory suppression indeed depends on the precision of forward models of the motor system, we should observe increased N1 attenuation in conditions of high as compared to low action-effect contingency.

2 Methods and materials

2.1 Subjects

Twenty-three healthy right-handed adults (20-32 years old, mean age 24 years, 11 female), with normal or corrected-to-normal vision participated in the after providing written informed consent, and in accordance with the Declaration of Helsinki.

2.2 Agency paradigm

A combination of an agency judgment paradigm (Linser & Goschke, 2007) and a sensory suppression paradigm (Martikainen, Kaneko, & Hari, 2005) was used, and the experiment consisted of three different tasks: the motor-effect (ME), the effect-only (E) and the motor-only (M) task (see Fig. 5.1). In the ME task, a visual stimulus was generated by the participant's action, whereas in the E task, the visual stimulus was externally generated and passively observed. By contrasting the ERP related to the visual stimulus in ME as compared to E, we aimed to quantify self-specific sensory suppression. The M task, in which the participant's action did not produce a visual stimulus, served as a control to rule out motor activity as a possible confounding factor in the comparison between the ME and E task.

In the ME task, participants responded to a target stimulus (circle or square, presented for 50 ms) with a left or right key press according to a fixed stimulus-response mapping (counterbalanced across participants) without speed instruction. The key press triggered a visual effect stimulus (with a delay of 20 ms) which consisted of a set of three arrows (500 ms) pointing either upwards or downwards. Visual stimuli were presented in black on a gray background subtending a visual angle of 0.5 x 2°. For each block of trials, participants were asked to observe and judge the relation between their action (left or right key press) and the type of effect stimulus (up or downward direction of the subsequent arrows).

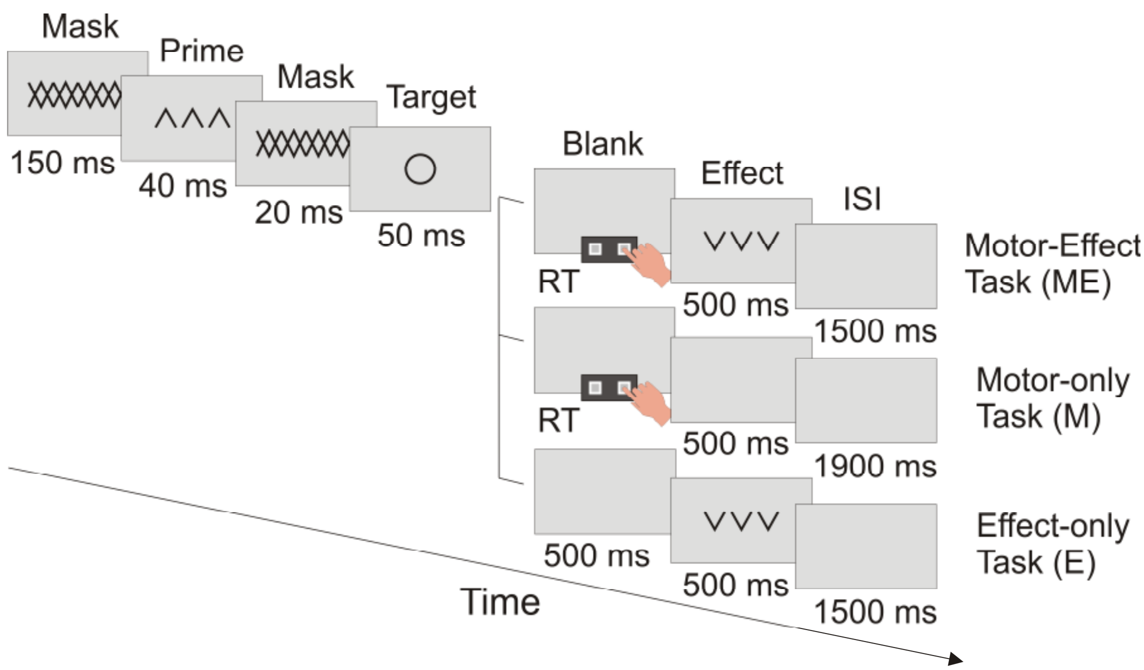

Figure 5.1. Schematic representation of the sequence of events during the ME, M and E task; examples of an incongruent prime-effect relation are shown.

The contingency between action and effect was varied; that is, the predictability of the type of effect stimulus on the basis of the action could be either high (75%) or low (50%). For example, in the high contingency condition, 75% of the up arrows were related to the left key and 25% to the right key (and vice versa for down arrows), whereas in the low contingency condition, up and down arrows were associated equally (50%) with both left and right key. This target-effect mapping was counterbalanced across participants. Importantly, we used priming in order to induce sensory anticipations prior to the action as a further experimental factor. Each trial started with the presentation of a mask stimulus (150 ms, composed of up and down arrows superimposed on each other) followed by the prime (40 ms) and another mask stimulus (20 ms). The prime stimulus was either identical to the future action effect (congruent priming) or consisted of arrows pointing in the opposite direction as the effect stimulus (incongruent priming). The interstimulus interval between action effect and forward mask was randomized between 1200 and 1800 ms. Both experimental factors, priming and contingency, were varied in blocks of 40 trials and participants performed three blocks for each condition (high contingency: congruent and incongruent priming; low contingency: congruent and incongruent priming). After each block of trials, participants judged the causal relation between their action (left/right key press) and the subsequent effect (up/down arrow) on a visual analog scale (VAS) ranging from 0 (no relation) to 100 (perfect relation). In total, participants performed 12 blocks of the ME task.

In the E task, participants passively watched the same visual stimuli used in the ME task, that is, without the instruction to press a key. The former effect stimuli were now externally generated by the computer with identical inter-stimulus timing as in the ME task. The factors contingency and priming were also varied in blocks of 40 trials, with a total of 12 blocks, as in the ME task. For each block, participants were asked to judge the causal relation between the target symbol (circle/square) and the subsequent effect stimulus (up/down arrows) on the same VAS ranging from 0 (no relation) to 100 (perfect relation). Thus, visual stimulation in E and ME was identical both in quality and in timing.

In the M task, participants had to respond to target stimuli exactly as in the ME task, but no visual effect was delivered following the action. Nine blocks of 18 trials were presented, and no (VAS) judgment was required at the end of each block. The ERP response in the M task was later compared with the ERP response in the ME task. The order of the tasks was fixed across all participants: Two blocks of ME and E were followed by one block of M and by a three minute break after every 11 blocks (ME-E-M-ME-E-M-ME-E-M-ME-E-break). This sequence of experimental blocks was repeated three times.

2.3 Prime processing & prime awareness tasks

After the main experiment, participants performed a response priming task (duration 3 min.) to assess cognitive processing of the prime stimuli. The task consisted of speeded forced-choice responses (left or right key press) to a target stimulus (up or down arrow). The target-response mapping (e.g., up arrow – left key) was kept equal to the response-effect mapping (left key - up arrow, respectively) of the ME task. Targets were preceded by masked primes (up or down arrows), as in the ME task, which could be either congruent or incongruent in relation to the target stimulus. Participants performed a random sequence of 60 congruent and 60 incongruent trials. Differences in reaction times depending on prime congruency would indicate that primes were indeed processed.

Prime awareness was first assessed using a subjective measure by systematically asking questions concerning the mask and target stimuli. Next, participants were informed of the nature of the prime stimulus and instructed to pay attention to the mask stimulus in order to perform a short forced-choice prime discrimination task as an objective measure of prime awareness. Trials consisted of masked prime stimuli only and participants were instructed to respond according to a fixed target-response mapping (e.g., up arrow – left key, down arrow – right key). Forty trials were presented, and primes appeared in random order. Prime visibility would be reflected in above-chance performance.

2.4 Electrophysiological recording and data analysis

The electroencephalogram (EEG) was recorded from 64 Ag-AgCl scalp electrodes (10-20 system, BioSemi Active II system, BioSemi, Amsterdam, Netherlands). The electro-oculogram (EOG) was obtained from electrodes placed external to the outer canthus of each eye and below and above the right eye. EEG and EOG signals were amplified and digitized online at a sampling rate of 512 Hz. Off-line data were re-referenced to average reference, low-pass filtered at 30 Hz and high-pass filtered at 0.75 Hz. All off-line analyses were performed using Brain Vision software (Brain Products GmbH, Gilching, Germany). Muscular and other non-stereotyped artifacts were excluded by visual inspection, stereotyped artifacts such as ocular and electrode artifacts were identified and removed using independent component analysis (ICA) (Jung et al., 2000).

The continuous data were segmented from –200 to 400 ms relative to onset of the effect stimulus and baseline corrected over the pre-response interval (-200 to 0 ms). The segmented data were then averaged across trials for each experimental task (ME, E, M), priming condition (congruent and incongruent priming) and contingency condition (high and low contingency) within each participant. Only trials with correct responses were included in average ERPs. Furthermore, ERP waveforms locked to effect-stimuli in the ME task were corrected for possible motor contamination (due to concurrence of response- and effect-related processes) by subtraction of activity in the M task. The corrected ERPs were used in all subsequent analyses such that the influence of motor activity as a confounding factor could be ruled out in the comparison of the E and ME task. Similar correction procedures have been applied by previous ERP studies on sensory suppression (Gentsch & Schütz-Bosbach, in press; Lange, 2011; Martikainen, Kaneko, & Hari, 2005).

In our analysis of the average ERP, we focused on the N1 component and quantified its mean amplitude at fronto-centro-parietal electrode sites (FC3, FCz, FC4, C3, Cz, C4, CP3, CPz, CP4) in the 80 to 130 ms time interval following the onset of the effect stimulus. The N1 component was selected for this analysis because it has been found to reflect self-specific suppression to auditory (Martikainen, Kaneko, & Hari, 2005) as well as visual sensory events (Gentsch & Schütz-Bosbach, in press; Schafer & Marcus, 1973).

2.5 Statistical Analyses

For the ERP data, a 3-way repeated measures analysis of variance (ANOVA) was run with the experimental factors task (2 levels: ME, E), anterior-posterior electrode location (3 levels: FC, C, CP) and lateral scalp location (3 levels: 3=left, z=midline, 4=right). Additional ANOVAs involving the factors contingency (2 levels: high, low) and priming (2 levels: congruent, incongruent) were conducted separately for the ME and E task. If data violated the sphericity assumption, Greenhouse-Geisser correction was applied. All measured amplitude values were tested for normal distribution with the Kolmogorov-Smirnov test. For causality ratings in the ME and E task, separate 2-way repeated measures ANOVAs were run with contingency and priming as experimental factors. Response accuracy and reaction times in the response priming were analyzed using repeated measures ANOVAs with the factor prime-target relation (2 levels: congruent, incongruent). Response accuracy in the prime detection task was analyzed by a one-sample t-test to determine whether subjects performed above chance. Post-hoc Tukey's HSD tests were performed in case of significant ANOVA findings.

3 Results

3.1 Causality judgments

As a measure of the sense of agency at the reflective level, participants judged the causal relation between their key press and the type of visual effect stimulus on a VAS scale. The means of the individual rating scores per condition are depicted in Figure 5.2.

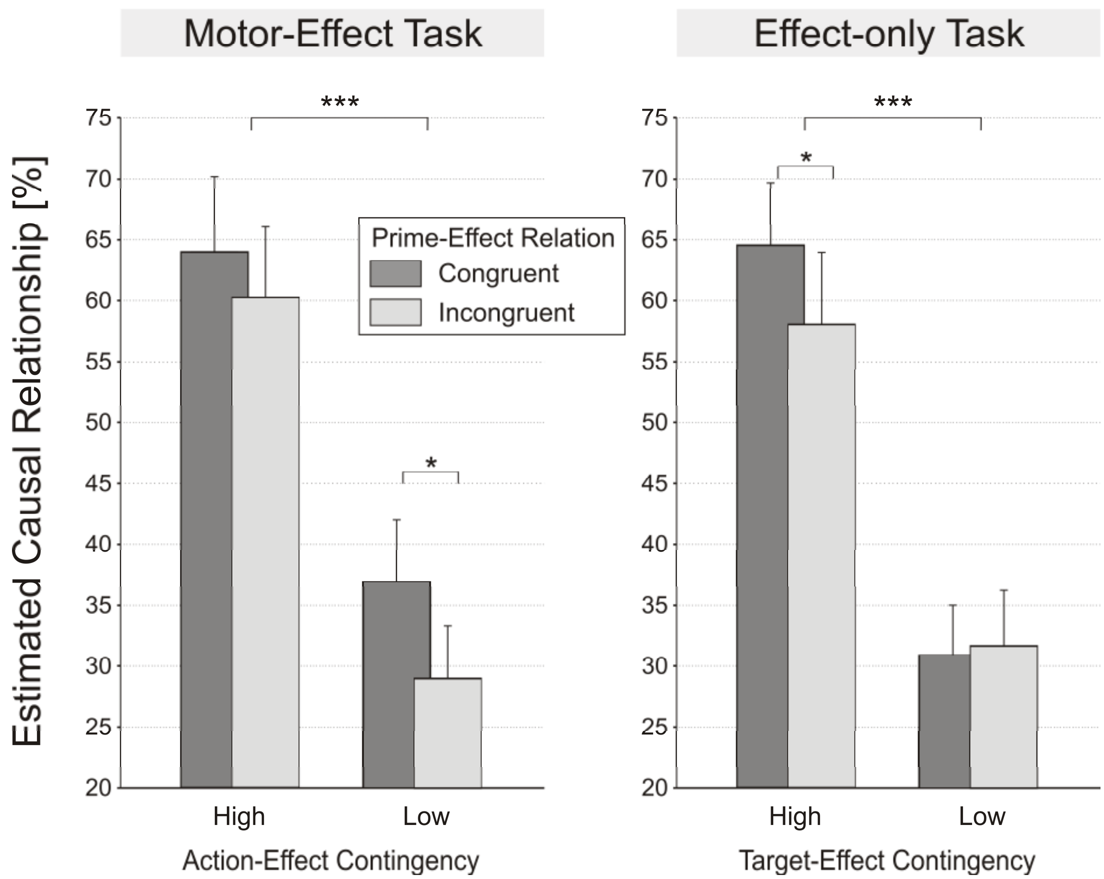

Figure 5.2. Mean judgments of agency in the ME task (left) and causality in the E task (right), separately for priming and contingency conditions.

Separate repeated measures ANOVAs were conducted for the ME and E task with the mean rating scores as the dependent variable involving the factors contingency (high, low) and priming (congruent, incongruent). For the ME task, there was a significant main effect of contingency, $F(1,22) = 88.73$, $p < .001$, due to larger rating scores in blocks of high contingency (M=62.1, SEM=2.62) as compared to low contingency (M=32.9, SEM=2.16). In the E task, the ANOVA also yielded a significant main effect of contingency, $F(1,22) = 111.52$, $p < .001$, with ratings being larger if contingency was high (M=61.7, SEM=2.88) as compared to low (M=32.2, SEM=2.38). The factor priming showed a significant influence in the ME task, $F(1,22) = 7.58$, $p < .05$, but only a trend effect in the E task, $F(1,22) = 3.36$, $p = .08$. That is, in the ME task, larger ratings were obtained for blocks of congruent priming (M=50.3, SEM=2.23) relative to incongruent priming (M=44.7, SEM=1.95), whereas in the E task, the difference between blocks of congruent and incongruent priming was less pronounced (M=48.5, SEM=2.36 vs. M=45.4, SEM=2.42).

The factors contingency and priming did not interact in the ME task. However, in the E task, the ANOVA showed a significant interaction effect, $F(1,22) = 5.08$, $p < .05$. This was due to a trend effect of priming (congruent vs. incongruent) which was present only in blocks of high contingency [M=65.4, SEM=2.96 vs. M=57.9, SEM=3.28, $p = .058$] but not low contingency [M=31.5, SEM=2.76 vs. M=32.8, SEM=2.71, $p = .96$]. An overall ANOVA with the factors task, contingency and priming yielded a significant three-way interaction, $F(1,22) = 5.39$, $p < .05$. Post hoc comparisons revealed that the direction of interaction between contingency and priming was reversed in the ME task relative to the E task. That is, in the ME task, a trend effect of priming (congruent vs. incongruent) was present in blocks of low contingency [M=36.9, SEM=2.79 vs. M=28.9, SEM=2.37, $p = .065$] but not in blocks of high contingency [M=63.6, SEM=3.26 vs. M=60.5, SEM=2.76, $p = .74$].

Furthermore, it was analyzed whether performance measures in the ME task were influenced by the experimental factors contingency and priming. No significant differences in mean reaction time or error rate was found between blocks of high and low contingency ($p > .3$ and $p > .4$) or congruent and incongruent priming ($p > .2$ and $p > .9$); hence, they cannot account for the differences observed in the VAS ratings.

3.2 Prime processing and prime awareness

Analysis of reaction time and response accuracy data in the response priming task revealed that prime stimuli influenced the participants' performance, confirming that primes were indeed processed. That is, reaction times were faster to targets that were primed by a congruent stimulus (*M*=428ms, *SEM*=12.58) as compared to an incongruent stimulus [*M*=462ms, *SEM*=15.94; $F(1,20) = 22.66$, $p < .001$]. Correspondingly error rates were lower for congruent trials (*M*=4.6%, *SEM*=1.11) as compared to incongruent trials [*M*=9.9%, *SEM*=2.49; $F(1,20) = 10.30$, $p < .01$].

Subjective measures revealed that primes were invisible. None of the participants reported having seen the masked primes either spontaneously or when questioned about the nature of the mask and target stimuli at the end of the agency experiment. However, after informing participants about the prime stimulus and instructing them to pay attention to them, an objective measure of prime visibility revealed that participants were able to discriminate the prime stimuli. Specifically, in the prime detection task, participants performed a forced-choice judgment (left/right) on the masked primes (up/down arrows) and the rate of correct responses was tested against chance performance (50% correct) using a one-sample t-test. Across all participants, the analysis revealed a significant result, indicating that prime stimuli were identified correctly in 65% of the cases [$t(22) = 3.72$, $p < .01$]. Hence, according to an objective forced choice criterion, prime stimuli obviously reached participants' awareness. That is, whereas under conditions of inattention, stimuli were invisible, they could be reported when participants' attention was focused on them, which indicates supraliminal priming.

3.3 Event-related potentials

Figure 5.3 displays the effect-locked ERP waveforms obtained for E and ME task. The N1 component is evident as a negative deflection peaking around 100 ms after onset of the effect stimulus, with a mid-central scalp distribution. The N1 wave appears to be larger in the E task as compared to the ME task.

The mean ERP voltages were subjected to an initial three-way repeated measures ANOVA across all priming and contingency conditions in order to quantify the sensory suppression effect in the visual ERP. The factors included task, anterior-posterior electrode location and lateral scalp location. The analysis yielded a significant main effect of the factor task on the N1 component, $F(2,44) = 5.4$, $p < .05$, indicating smaller amplitudes in the ME as compared to the E task. This result replicates findings of self-specific N1 suppression in the auditory and visual modality. Further, the factor anterior-posterior electrode location had a significant impact, $F(2,44) = 3.96$, $p < .05$, due to larger N1 amplitudes over fronto-central as compared to centro-parietal brain regions, $p < .05$. No effect of laterality was obtained and there was no significant interaction between task and electrode site.

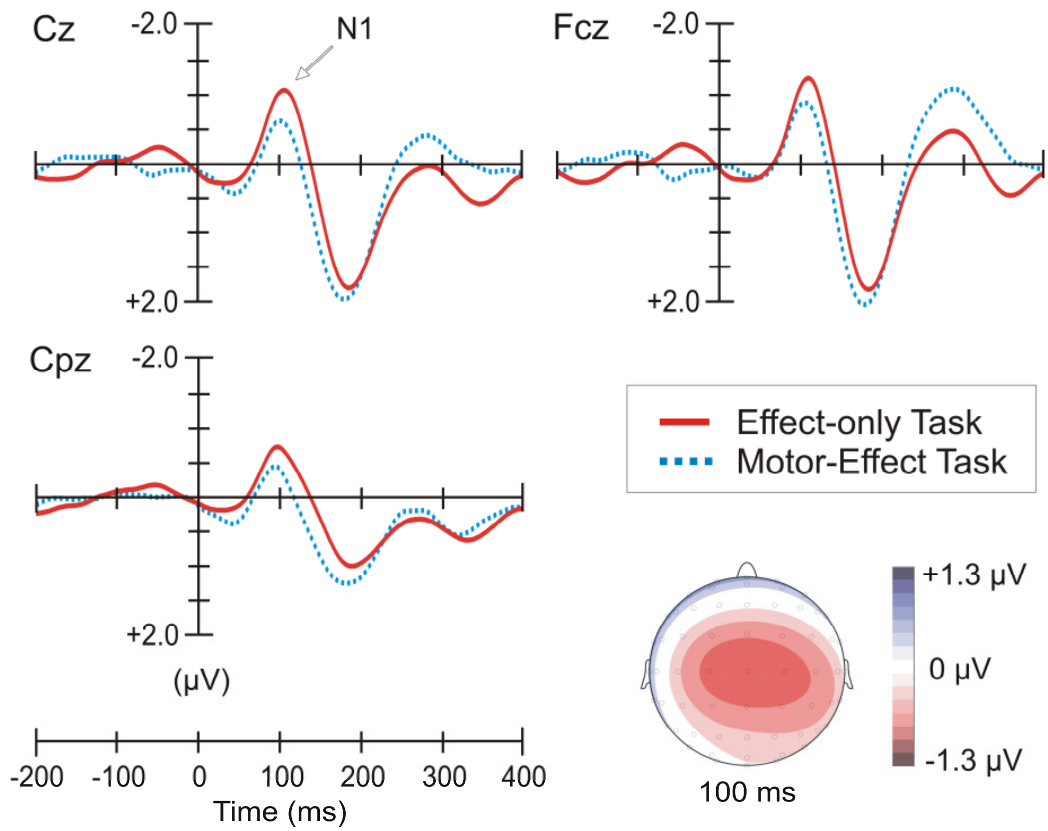

Figure 5.3. Stimulus-locked grand average ERPs during active generation of visual effects (ME task, dotted lines) and passive observation of externally generated visual effects (E task, solid lines) at electrodes FCz, Cz and Cpz, and scalp topographies of the voltage difference between E and ME task.

In order to investigate the differential effects of priming and contingency on N1 amplitudes, separate ANOVAs were computed for the ME and E task, including the factors priming, contingency, anterior-posterior electrode location and laterality. Figure 5.4 shows grand-average ERP waveforms for the ME task and the E task at electrode Cz as a function of priming and contingency.

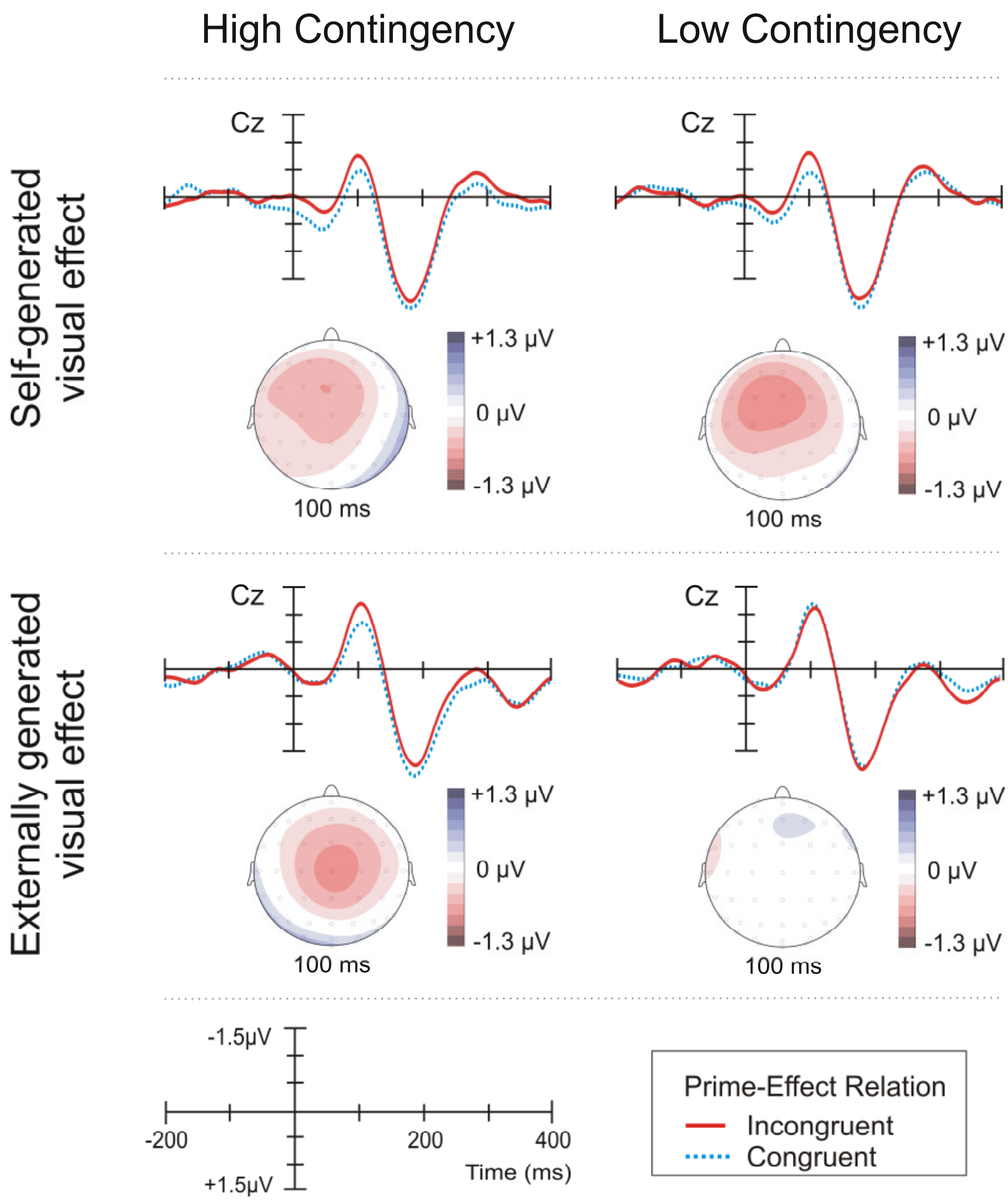

Figure 5.4. Grand average ERPs to visual effects preceded by congruent primes (dotted lines) or incongruent primes (solid lines), separately for conditions of high contingency (left) and low contingency (right) in the ME task (upper part) and E task (lower part) at the vertex electrode (Cz). Scalp topographies of the voltage difference between congruent and incongruent primes are shown.

In the ME task, the analysis revealed a significant main effect of the factor priming on N1 amplitude, $F(1,22) = 8.25$, $p < .01$, indicating smaller amplitudes for congruent as compared to incongruent priming. No interaction of priming and electrode location was observed, indicating that the effect of priming was present at all electrode sites. Furthermore, the main effect of contingency was not significant, $F(1,22) = 0.91$, $p = .35$; however, a significant interaction between contingency and anteriority-posteriority was observed, $F(2,44) = 4.30$, $p < .05$. This was due to the fact that N1 amplitudes were larger in blocks of low as compared to high contingency but only at fronto-central sites ($p < .01$), and not at central or centro-parietal sites. Priming and contingency did not interact significantly, $F(1,22) = 0.08$, $p = .77$, indicating that the effect of priming was present no matter whether contingency was high or low.

For the E task, the ANOVA yielded no significant effect of the factor priming, $F(1,22) = 2.15$, $p < .16$, or of the factor contingency, $F(1,22) = 0.83$, $p = .37$. However, there was a significant interaction effect between priming and contingency, $F(1,22) = 6.19$, $p < .05$, indicating that congruent priming elicited smaller amplitudes than incongruent priming but only in blocks of high contingency ($p > .05$) and not in blocks of low contingency ($p = .96$). Furthermore, we observed a three-way interaction between priming, contingency and laterality, indicating that the difference between priming conditions in high contingency blocks was only present at midline electrodes ($p < .001$) and not at left and right sites.

Together our results so far show N1 suppression of the visual ERP specifically to self-generated stimuli (ME) relative to externally generated events (E). Further analyses showed N1 modulation by priming in the ME but not in the E task and N1 modulation by an interaction between priming and contingency in the E but not in the ME task. In order to test whether priming or contingency had an impact on the suppression effect, an ANOVA was performed with amplitudes of the difference waves between E and ME task centered at central electrode. However, neither the main effect of priming ($p = .28$) and contingency ($p = .54$) nor the interaction between both ($p = .19$) reached significance.

4 Discussion

Perceiving that the occurrence of a sensory event in the environment obviously depends on our actions will lead to an experience of agency and a feeling of control for this event. This experience is immediate and remains mostly unconscious but we can become aware of it and explicitly judge whether we did or did not cause the event. It has been proposed that the sense of agency depends on the ability to make predictions about the sensory consequences of an action. The present study reveals that motor and nonmotor predictions are weighted differently depending on their reliability and depending on the level of agency processing. In the following, we will discuss our findings separately for the two levels of agency representation, the reflective and pre-reflective experience of agency.

4.1 Reflective agency experience

At the reflective level of agency, our results show that the agency system relies on prime-induced sensory expectations in situations where no reliable and precise motor-related predictions of the action consequence are available. That is, participants judged the causal strength between action and effect to be larger when expectations of the upcoming action effect were induced by priming. However, this effect was present only if contingency between action and effect was low, meaning that the specific type of visual event could not be predicted based on the action. Hence, our data provides evidence for the hypothesis that optimal cue integration underlies the sense of agency (Synofzik, Vosgerau, & Lindner, 2009). Nevertheless, despite the influence of nonmotor expectations, the explicit judgment of agency was most strongly modulated by precise motor predictions due to the contingency relation between the action and a specific sensory consequence. This is in line with studies showing that the contingency rule between a potential cause (i.e., action) and a specific effect is a major determinant for human causal learning and judged causality (Elsner & Hommel, 2004; Shanks & Dickinson, 1991).

Our results seem to be inconsistent with some previous findings (Sato, 2009) suggesting additive effects of nonmotor and motor expectations. In the study by Sato (2009), participants performed a similar forced choice reaction task in which action effects were primed semantically, and were highly contingent (75% probability) upon the action or not (50% probability). Moreover, in this study, participants were told that the effect could either be caused by themselves or another person. Participants were then asked to judge their experience of authorship on a visual analogue scale. In contrast to our results, authorship judgments were more strongly enhanced by priming induced anticipations in conditions of high action-effect contingency; that is, where precise motor predictions were available. An explanation for the discrepancy in results might be that the presence of another agent in the study by Sato (2009) created a context of increased uncertainty, whereas in our paradigm no other agent was involved. That is, in Sato's low contingency condition, participants not only experienced the absence of reliable, precise motor-related predictions but also the presence of a potential alternative causal factor. Hence, it might be argued that there is a certain window of ambiguity regarding causality in which additional information is recruited to judge the cause of a sensory event. If certainty about causality is too high or too low, for example, due to the presence of several contextual or internal indicators, there is no need to rely on additional, alternative agency cues.

This interpretation is supported by our data from the observational control condition (i.e., E task) in which no embodied signals (i.e., no efferent cues, and hence motor predictions) were available at all, and causality judgments had to be exclusively based on contingency rules involving external sensory events only. In this context, the perceived causality was also enhanced by prime-induced sensory expectations, although only in conditions of high contingency and not in conditions of low contingency. These results indicate that if embodied signals are absent and alternative contingency rules are not reliable, the perceived causality between events cannot be modulated further by additional predictive mechanisms. Together, our findings suggest that explicit judgments of causality are a function of sensory predictions derived from embodied signals, probabilistic contingencies and sensory preview weighted differently depending on their reliability and the degree of uncertainty in a given context.

4.2 Pre-reflective agency experience

Furthermore, we measured N1 attenuation as a means to examine the immediate, pre-reflective level of agency representation. We replicated previous findings of reduced N1 amplitudes specifically linked to self-generated stimuli (Curio, Neuloh, Numminen, Jousmaki, & Hari, 2000; Martikainen, Kaneko, & Hari, 2005; Schafer & Marcus, 1973) with the control that the temporal and spatial occurrence of the stimulus could also always be predicted based on visual cues in conditions in which the stimulus was externally produced. N1 amplitudes were further reduced by congruency between prime and effect stimulus, suggesting that nonmotor sensory expectations influence the pre-reflective level of agency registration, which confirms findings of previous studies (Gentsch & Schütz-Bosbach, in press; Moore, Wegner, & Haggard, 2009). This effect of prime-induced expectations did not depend on the precision of the internal forward model of the motor system. That is, effect priming modulated N1 amplitudes in the presence of embodied signals (i.e., efferent information) independent of the specific relations between certain types of actions and sensory events. In other words, the mere presence of embodied signals seems to trump highly precise predictions based on specific contingency rules. In contrast, in the absence of embodied signals, the influence of prime-induced sensory expectations was much weaker, and in fact, was dependent upon additional contingency information, which mirrors our findings at the level of reflective causality judgments.

Importantly, our data cannot support the notion that the amount of sensory suppression reflects the precision of forward model predictions of the motor system. N1 amplitudes were unaffected by whether or not the exact shape of the visual event following the action could be predicted on the basis of contingency information. In fact, current research in humans still lacks a clear understanding of the exact nature of the predictive and filtering mechanism behind self-specific sensory suppression. One line of evidence supports the view that the amount of attenuation is proportional to the discrepancy between predicted and actual sensory feedback (Blakemore, Frith, & Wolpert, 1999; Blakemore, Wolpert, & Frith, 2000; Blakemore, Wolpert, & Frith, 1998, 2002). Other studies, however, found sensory suppression even when the details of the sensory consequence, for example, in terms of its intensity or temporal occurrence, could not be precisely predicted based on the action (Lange, 2011; Tsakiris & Haggard, 2003).

Recently, it has been proposed that there might be two separate mechanisms underlying sensory suppression, a fixed modulation of sensory input based on the mere presence of efference, and a proportional modulation based on precise predictions of a forward model if available (Tsakiris, Haggard, Franck, Mainy, & Sirigu, 2005). They argue that for the fixed “sensory bias”, an intention to act would be sufficient because the bias arises at early stages of action planning “before the precise details of the impending movement are determined” (p. 393). Indeed, a recent study (Voss, Ingram, Haggard, & Wolpert, 2006) showed that sensory suppression appears to rely on signals related to action preparation and not on the final motor command dispatched from the primary motor cortex. Hence, the attenuation of early N1 amplitudes here might reflect this process of self/nonself distinction labeling an action and its consequence as “mine” based on the mere presence of embodied signals, whereas the precise nature of the action consequence is evaluated later in sensory processing. This is consistent with ERP research on the visual mismatch negativity (MMN) showing that the detection of deviation from expected stimulus features is realized at later stages of sensory processing, in the latency range of the N2 component around 200 ms following a sensory event (Pazo-Alvarez, Cadaveira, & Amenedo, 2003).

Alternatively, one might argue that the extent to which highly accurate and precise predictive models are effective depends upon contextual factors (e.g., a noisy environment) and the type of sensory event. For example, for proximal, bodily sensory events which are in close relation to the effector, such as touch or speech, the level of specificity of the forward model might be higher regarding the intensity, temporal and spatial parameters of the event. Indeed, attenuation of self-administered tactile stimulation has been shown to strongly depend upon precise temporal and spatial predictions and proximity of the upcoming tactile sensation (Blakemore, Frith, & Wolpert, 1999).

In contrast, for distal, extracorporeal effects of actions such as sounds or visual stimuli produced by button presses, highly precise predictions might even be disadvantageous because of more variance or noise in the sensory outcome. For example, in the study by Tsakiris (2003), a participant’s key press caused a TMS pulse over the motor cortex which induced a finger twitch as the final somatic effect of the action. They found self-specific suppression to be unaffected by predictability of the stimulus intensity. Similarly, a recent study (Lange, 2011) showed that the amount of sensory suppression for sounds produced by key presses did not differ between predictable versus unpredictable sounds. That is, predictive models for distal sensory events involving external effectors (e.g., mechanical devices or another human actor) need to deal with differing and unknown intrinsic dynamics. Hence, due to potential delay, additional noise or nonlinearity in the expected outcome, predictions might be less specific in these contexts as compared to those, for example, that concern one’s own motor apparatus.

5 Conclusion

In summary, our study provides evidence for the hypothesis that optimal cue integration underlies the sense of agency (Synofzik, Vosgerau, & Lindner, 2009). The findings suggest that the sense of agency is based on different cues such as embodied signals, probabilistic contingency rules and sensory preview, which are combined in a way that each source of information is weighted differently depending on its reliability and the availability of alternative cues. We show that explicit judgments of agency are enhanced by sensory expectations arising from nonmotor systems. This influence was most strongly present in situations where no reliable and precise motor-related predictions of the action consequence were available and it further depended upon the general degree of uncertainty in a given context. However, despite the impact of nonmotor expectations, specific contingency rules between actions and effects were the major determinant of explicit causality perception. In contrast, sensory suppression as a pre-reflective marker of the sense of agency was modulated by nonmotor sensory expectations independent of precise internal forward models of the motor system. We conclude that the attenuation of neural responses to distal, extracorporeal action consequences is based primarily on embodied signals. The mere presence of efferent signals enables a first and immediate discrimination of sensory events as being self-caused or not, thereby mediating the primary, pre-reflective experience of “mineness” for a sensory event. This sensorimotor mechanism is then complemented further evaluation of the nature of the action consequence with respect to specific internal motor predictions as well as general beliefs about control so as to establish a strong experience of agency at higher cognitive levels.

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6 Manuscript of Study 3

Dysfunctional Forward Model Mechanisms and Aberrant Sense of Agency in Obsessive-Compulsive Disorder

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Abstract

Background: Patients with obsessive-compulsive disorder (OCD) lack the experience of action completion and agency. This subjective experience has been shown to depend on the integrity of predictions of action outcomes generated by forward models of the motor system. Motor predictions are critical for inhibitory gating of actions and their consequences, and abnormal activity in motor control circuits, including basal ganglia and premotor cortex, has been found in OCD. This is the first study explicitly investigating forward model mechanisms in OCD.

Methods: To test whether inhibitory gating based on motor predictions is physiologically altered in OCD, we used electroencephalography to measure N1 suppression during active generation and passive observation of visual feedback in

18 OCD patients and 18 healthy control subjects. Predictability of action feedback was manipulated on the basis of action and external cues, and simultaneous agency judgments were assessed.

Results: OCD patients did not show the typical N1 suppression to actively generated feedback as compared to passively observed feedback. Moreover, in OCD patients, the N1 was not modulated by additional predictive motor cues as observed in control subjects. If explicitly asked to report agency experience, enhanced estimations were found in patients, which correlated with the strength of incompleteness feelings.

Conclusions: OCD patients fail to predict and suppress the sensory consequences of their own actions. The constant mismatch between expected and actual outcome caused by this forward model dysfunction may explain the persistent feeling of incompleteness even after properly executed actions and the obsessed searching for control in these patients.

1 Introduction

The experience of completion and satisfaction associated with an action and its consequences is at the basis of perceiving ourselves as self-determined agents capable of causing and controlling events in our environment. In obsessive-compulsive disorder (OCD), a lack of agency is recognized as a central clinical feature and well documented in “not just right” experiences (Coles, Frost, Heimberg, & Rheaume, 2003; Leckman, Walker, Goodman, Pauls, & Cohen, 1994) or an inner sense of imperfection and incompleteness (Pitman, 1987). Patients with OCD report, for example, that when actively closing a door, even though they know it is closed, the feeling remains that it may not be properly closed, and this is accompanied by the impulse to go back and double-check. The neurocognitive underpinnings of agency experience are extensively studied in schizophrenia (Frith, 2005; Heinks-Maldonado et al., 2007; Synofzik, Thier, Leube, Schlotterbeck, & Lindner, 2010), however, to date there are no reports in OCD.

One important signal for the sense of agency is thought to arise from motor control processes (Blakemore, Wolpert, & Frith, 2002), in particular, from forward models of the motor system (Wolpert & Ghahramani, 2000). These internal models generate predictions of the sensory consequences of an action which can be used for motor control (Frith, Blakemore, & Wolpert, 2000; Wolpert, 1997): A comparison of predictions and intended outcome serves online monitoring of goal-achievement, whereas a comparison with the actual feedback provides a mechanism for filtering sensory input and for establishing a sense of agency (Blakemore, Wolpert, & Frith, 2000; Frith, 2005; Sato & Yasuda, 2005). Several research lines have related these two comparators to distinct neural systems, in particular, a frontal-medial system monitoring attainment of “high-level” goals and a posterior-parietal system serving online, fine-tuned motor adjustments (Desmurget et al., 1999; Krigolson & Holroyd, 2006). A dysfunctional frontal-medial system (Endrass, Klawohn, Schuster, & Kathmann, 2008; Gehring, Himle, & Nisenson, 2000; Riesel, Endrass, Kaufmann, & Kathmann, 2011; Ursu, Stenger, Shear, Jones, & Carter, 2003) and functional abnormalities in brain regions underlying motor control (Greenberg et al., 2000; Mantovani et al., 2006; Yucel et al., 2007) have been consistently associated with OCD. However, no study has yet explicitly investigated the functional integrity of forward models in OCD.

The function of these internal forward model predictions can be explored by measuring predictive inhibitory gating in sensory processing. In healthy adults, self-generated sensory events are typically suppressed as compared to externally generated events due to a precise cancellation of afferent input by forward predictions (ie, corollary discharge) of the motor system (Blakemore, Wolpert, & Frith, 2000; Sperry, 1950; von Holst & Mittelstaedt, 1950; Wolpert & Ghahramani, 2000). This mechanism of sensorimotor gating underlies the capacity to discriminate accurately between self-produced and external stimulation and thereby contributes to the sense of agency. In human electrophysiological studies, sensory suppression has been observed as a reduction of the N1 component of the event-related potential (ERP) to self-generated as compared to passively experienced sounds (Curio, Neuloh, Numminen, Jousmaki, & Hari, 2000; Ford & Mathalon, 2004; Numminen, Salmelin, & Hari, 1999) or visual events (Gentsch & Schütz-Bosbach, in press; Schafer & Marcus, 1973).

Interestingly, imprecise motor predictions have been found in patients with schizophrenia and suggested to cause delusional misattribution of control to external agents (Frith, 2005). In OCD, in contrast, cognitive theories have postulated elevated responsibility to be at the core of the disorder, that is, an overestimation of personal causal influence on events that are in fact beyond control (Rachman, 2002; Salkovskis, 1999; Salkovskis, Shafran, Rachman, & Freeston, 1999). The contribution of sensorimotor cues to the formation of such high-level judgments of one's own agency remains unclear. Recent models (Synofzik, Vosgerau, & Newen, 2008b) suggest that at low levels of agency registration, mechanisms of sensorimotor integration establish a pre-reflective experience of coherent sensory-motor flow and action completion. In contrast, at higher cognitive levels, an explicit judgment of agency is thought to be informed primarily by cognitive cues (eg, control and responsibility beliefs) and rationalization of sensory experiences. Therefore, in this view, ambiguous bottom-up sensory signals may not necessarily cause external misattribution of agency as proposed in the pathophysiology schizophrenia (Frith, 2005).

In the present study, we aimed at testing whether OCD patients show alterations in predictive sensory gating by measuring N1 suppression in the visual ERP during active self-generation of visual events compared with passive observation of the same events. By varying the probabilistic contingency of action and outcome, and by priming the visual outcome prior to the action, this paradigm furthermore allowed us to examine the integrity of motor-related and unrelated sensory predictions. Additionally, we analyzed explicit judgments of agency during the task. We hypothesized that gating of sensory information on the basis of motor predictions would be reduced in OCD patients, due to a dysfunctional system of motor control. Moreover, behavioral studies have shown that illusions of control and inflated responsibility in OCD may serve as compensatory mechanisms for restoring a threatened sense of control (Moulding & Kyrios, 2006; Reuven-Magril, Dar, & Liberman, 2008). Therefore, as opposed to schizophrenic misattributions of agency, judgments of agency in OCD were expected to be enhanced.

2 Methods and Materials

2.1 Subjects

Eighteen patients with OCD and 18 age- and gender-matched healthy control subjects participated in the study (Table 6.1). Patients were recruited from the outpatient clinic for OCD at the Department of Clinical Psychology, Humboldt-Universität zu Berlin, Germany. All patients met *DSM-IV* diagnostic criteria for OCD as the primary clinical diagnosis, which was examined by experienced clinicians using the Structured Clinical Interview for *DSM-IV* (SCID; First, Spitzer, Gibbon, & Williams, 1996). Further inclusion criteria were: (1) absence of alcohol or substance abuse or dependence; (2) absence of major internal or neurological disorders; (3) absence of psychotic symptoms; (4) being medication free or stable on their medication dose for at least 1 month. Thirteen patients were taking psychotropic medication (selective serotonin reuptake inhibitors, SSRI; tri-/tetracyclic antidepressants, TCA/TeCA). Healthy control participants were included if they presented no evidence of current or past psychopathologic or neurologic disorders. All participants gave written informed consent to a protocol approved by the local ethics committee and received €8 per hour for their participation.

Table 6.1. Demographical and Clinical Characteristics of OCD and Control Groups

	OCD (n = 18)	Control (n = 18)		
	Mean (SD)	**Mean SD**	**$X^2(1)$ / t(36)**	**p-value**
Demographic Data				
Age, y	35.4 (9.5)	37.4 (9.8)	-0.60[b]	0.55
Percent Female, %	33.3 (n/a)	33.3 (n/a)	0.00[a]	1.00
Verbal IQ	109.8 (8.9)	107.4 (10.6)	0.75[b]	0.46
Clinical Characteristics				
Onset of illness, y	18.5[c] (7.2)	n/a	n/a	n/a
BDI-II	12.7 (10.8)	4.4 (6.9)	2.70[b]	0.01
MADRS	8.9[c] (7.3)	n/a	n/a	n/a
STAI-T	39,7 (12.3)	34.7 (8.6)	1.41[b]	0.17
STAI-S	47.0 (13.6)	35.5 (11.7)	2.68[b]	0.01
OCI-R, total	21.2 (13.4)	7.7 (7.3)	3.76[b]	0.001
Y-BOCS, total	16.8[c] (6.3)	n/a	n/a	n/a
Y-BOCS, Obsessions	8.9 (2.9)	n/a	n/a	n/a
Y-BOCS, Compulsions	7.9 (3.9)	n/a	n/a	n/a
OC-TCDQ,				
harm avoidance	8.2 (4.2)	n/a	n/a	n/a
incompleteness	12.2 (6.5)	n/a	n/a	n/a
	No. (%)			
Medication at study time				
Medication free (>4 wk)	5 (27.8)			
Paroxetine (SSRI)	6 (33.3)			
Citalopram (SSRI)	3 (16.7)			
Escitalopram (SSRI)	2 (11.1)			
Trimipramin (TCA) with SSRI	1 (5.6)			
Mirtazapin (TeCA)	1 (5.6)			

Abbreviations: BDI, Beck Depression Inventory; MADRS, Montgomery-Asberg Depression Rating Scale; OCI-R, Obsessive-Compulsive Inventory Revised; STAI-S/T, Spielberger State-Trait Anxiety

Inventory-State/Trait Form; Y-BOCS, Yale-Brown Obsessive-Compulsive Scale; OC-TCDQ, Obsessive-Compulsive Trait Core Dimension Questionnaire; NA, not applicable; SSRI, selective serotonin reuptake inhibitor; TCA/TeCA, tri-/tetracyclic antidepressant.
[a] chi-square test; [b] independent samples *t* test; [c] assessed in 16 OCD patients.

2.2 Questionnaires

To assess severity and characteristics of OCD psychopathology, we administered the Yale-Brown Obsessive-Compulsive Scale (Y-BOCS)(Goodman et al., 1989) and the Obsessive-Compulsive Inventory Revised (OCI-R)(Foa et al., 2002). Depressive symptoms were assessed using the Montgomery-Asberg-Depression Rating Scale (Montgomery & Asberg, 1979) and the Beck-Depression-Inventory (BDI-II)(Beck, Steer, & Brown, 1996). In addition, the State-Trait Anxiety Inventory (STAI)(Spielberger, Gorsuch, & Lushere, 1970) was administered to assess state and trait level anxiety. Feelings of incompleteness and harm avoidance related to obsessions or compulsions were assessed using the Obsessive-Compulsive Trait Core Dimension Questionnaire (OC-TCDQ)(Summerfeldt, Kloosterman, Parker, Antony, & Swinson, 2001). Verbal intelligence was measured by a German vocabulary test (Schmidt & Metzler, 1992).

2.3 Agency Paradigm

Participants performed a modified version of an agency paradigm that has been described in detail elsewhere (Gentsch & Schütz-Bosbach, in press) and which consisted of three different tasks (see Figure 6.1).

In a motor-effect task (ME task), subjects self-triggered a visual effect stimulus (red or blue square) with a left or right key press according to a fixed target-response mapping without speed instruction. During blocks of high action-effect contingency, in 75% of the trials, a particular effect-stimulus (eg, blue) appeared when a particular key was pressed (eg, left key); in the remaining 25% of the trials the other effect-stimulus appeared (eg, red). During blocks of low action-effect contingency, both effect-stimuli were associated equally (50%) with both left and right key presses. Participants' made judgments of the causal relation between their action and the effect on a visual analog scale (VAS) ranging from 0 (no relation) to 100 (perfect relation) after 40 trials of one experimental block had been completed. In addition, prior to each key press, a semantic prime stimulus was presented. That is, each trial began with the presentation of a prime stimulus (consisting of the words “BLUE” [German: “BLAU”] or “RED” [German: “ROT”]) followed by a mask stimulus (composed of a meaningless letter string, XZXZXZ). The relation between prime and effect was either congruent or incongruent depending on whether prime and effect denoted the same or different colors. The factor priming (congruent, incongruent) was realized in blocks of 40 trials, in a fully crossed 2x2 design with the factor contingency.

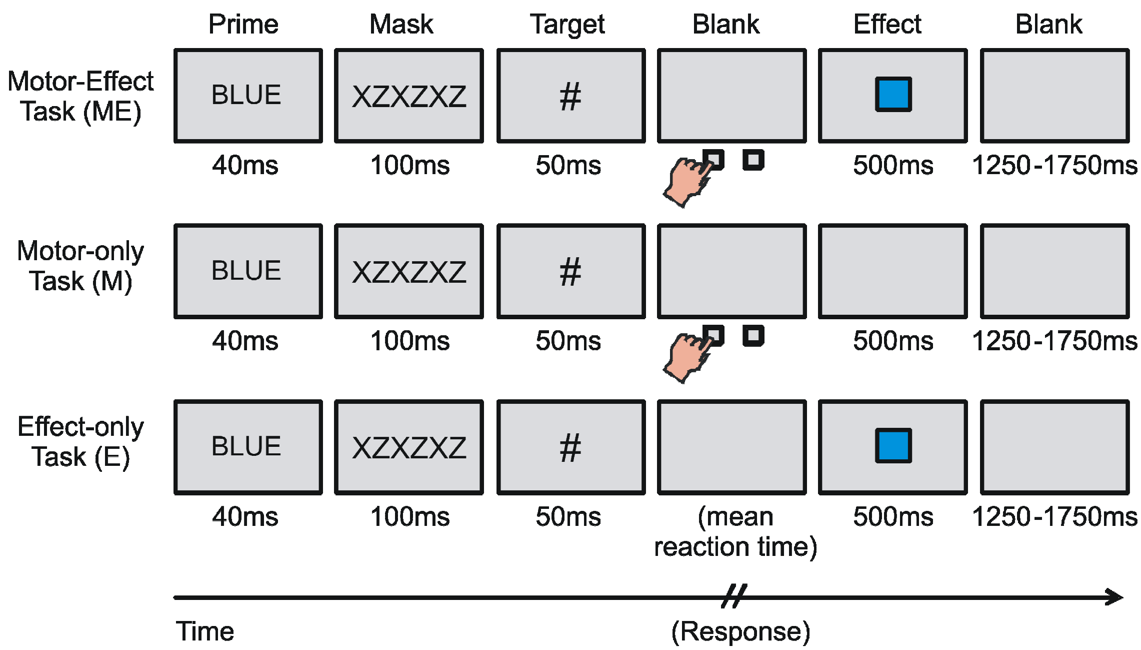

Figure 6.1. Schematic representation of the sequence of events during the ME, M and E task; examples of a congruent prime-effect relation are shown.

In an effect-only task (E task), participants merely watched the visual effect stimulus without performing a key press, and were instructed to judge the causal relation between a particular target symbol (“#” or “+”) and the subsequent effect stimulus (red or blue square). All other features remained the same as in the ME task, including prime-effect relations and target-effect contingencies. The E task was carried out to compare cortical responses during passive observation versus self-generation of sensory events in order to measure self-specific sensory suppression. The ME task and E task consisted of 320 trials each, presented in eight blocks of 40 trials (two blocks per contingency x priming condition).

In a motor-only task (M task), visual stimulation and participants' responses were the same as in the ME task, except that no visual effect stimulus followed the key press and no causality judgment had to be performed. This condition served to obtain and remove motor activity as a possible confounding factor in the comparison between the ME and E task. The M task consisted of 160 trials presented in four blocks of 40 trials each. The order of the tasks was fixed across all participants: Two alternating blocks of ME and E were followed by one block of M task. This sequence of blocks (ME-E-ME-E-M) was repeated four times. To familiarize participants with the tasks and with causality judgments, they completed two high contingency blocks of ME and E prior to EEG recording. The total duration of the agency judgment experiment was 45 minutes.

2.4 EEG Recording and ERP Analysis

The electroencephalogram (EEG) was acquired from 61 channels using Brain Vision Recorder software (Brain Products GmbH, Gilching, Germany), with a 250 Hz sampling rate and the vertex electrode (Cz) as recording reference. Impedances were kept below 10 kΩ. Off-line EEG signals were re-referenced to average reference and subjected to a 0.75-30 Hz band-pass filter. Artifact correction was carried out by manual rejection and independent component analysis (Jung et al., 2000). Only trials with correct button presses occurring 200-1500 ms after the target stimuli (99% of the total trials) were included in the analysis. Stimulus-locked epochs were extracted from the continuous data, baseline corrected over the pre-response interval (-200 to -100 ms), and averaged separately for each participant, condition and site. To cancel out movement-related potentials in the ME task, difference waves were calculated by subtracting the ERPs in the M task from the ERPs in the ME task. This procedure allowed the direct comparison of ERPs in the E and ME task for measuring self-specific sensory suppression ruling out motor activity as a confounding factor (Gentsch & Schütz-Bosbach, in press; Lange, 2011; Martikainen, Kaneko, & Hari, 2005).

Our main electrocortical dependent measure was the amplitude of the N1 component. Because the visual N1 was noted to include functionally separable anterior and posterior subcomponents (N1a and N1p) with different latencies (Vogel & Luck, 2000), distinct measurement windows and sites were chosen. The N1 was quantified as the mean amplitude within the 80-130 ms time window at the vertex (Cz; for N1a), and within the 140-200 ms time window at occipito-parietal sites (O1, O2, PO3, PO4; for N1p).

2.5 Statistical Analyses

For causality ratings in the ME task and E task, separate mixed 2 x 2 x 2 analyses of variance (ANOVAs) were run with group (OCD patients, controls) as the between-subject factor and contingency (high, low) and priming (congruent, incongruent) as within-subject factors. For the ERP data, a mixed 5-way ANOVA was run with the between-subjects factor group (OCD patients, controls) and within-group factors task (ME, E), contingency (high, low), priming (congruent, incongruent) and electrode site. The Greenhouse-Geisser correction was applied in cases that the data violated the sphericity assumption. Post hoc Newman-Keuls tests were performed in cases of significant ANOVA findings. Associations between sensory suppression effects and symptom measures or agency judgments were examined by Pearson product-moment correlations.

3 Results

3.1 Demographic and Clinical Characteristics

Demographic data and clinical characteristics are summarized in Table 6.1. Groups did not differ significantly with respect to age, gender and verbal intelligence. OCD patients were characterized by a mild to moderate level of OCD symptoms (as indicated by YBOCS scores) and, on average, subclinical levels of depressive symptoms.

3.2 Agency Judgments

To evaluate whether groups differed in their explicit judgments of agency, VAS ratings were analyzed. Figure 6.2 shows the mean rating scores in the ME and E condition. A mixed ANOVA with group, task, priming condition and contingency condition was conducted.

Ratings of causality across patients and control subjects were significantly higher when effects were expected in conditions of high contingency and congruent priming as compared to low contingency ($F_{1,34}$=99.67; P<.001) and incongruent priming ($F_{1,34}$=8.34; P=.007). Patients' ratings of agency and causality were marginally higher (mean [SD], 38.3 [13.3]) than those of control subjects (mean [SD], 30.3 [13.7]; $F_{1,34}$=3.67; P=.06).

To evaluate group differences specifically for agency judgments during self-generation of visual effects, a separate ANOVA for the ME task was conducted. Patients and control subjects differed marginally in the impact of prime induced anticipations on agency judgments, depending on the level of contingency ($F_{1,34}$=3.09; P=.08). Post hoc Newman-Keuls tests revealed that control participants showed higher agency ratings after congruent than incongruent priming only in blocks of high contingency (P=.003; mean [SD], 53.2 [19.1] vs 39.9 [19.3]) but not low contingency (P=.81; mean [SD], 12.8 [12.3] vs 11.8 [11.7]). In contrast, agency ratings of patients with OCD remained unaffected by priming in both the high (P=.84; mean [SD], 54.1 [20.9] vs 53.3 [15.3]) and low contingency (P=.46; mean [SD], 21.9 [21.7] vs 18.8 [18.6]) conditions.

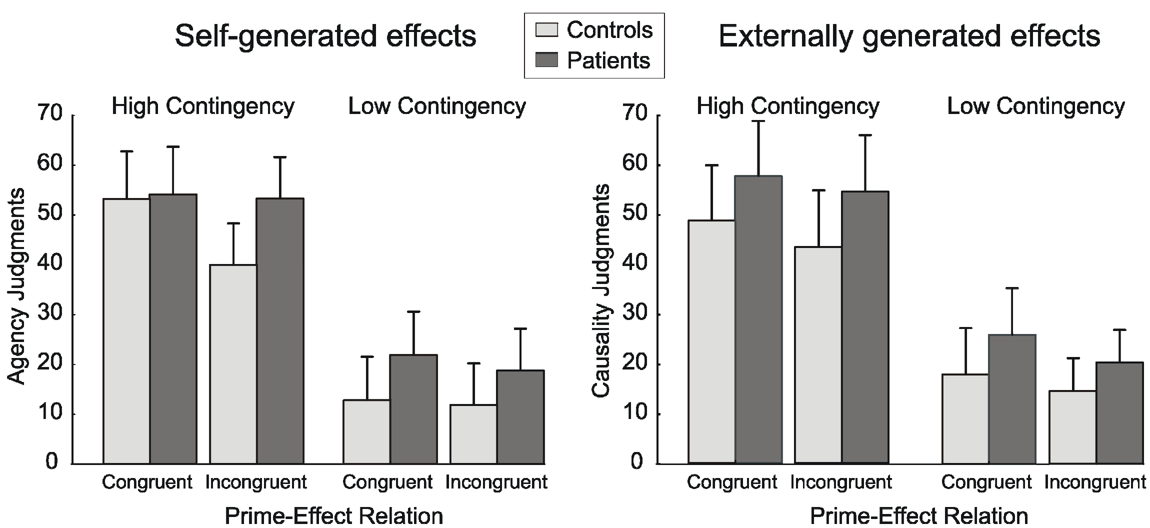

Figure 6.2. Mean judgments of agency in the ME task (left) and causality in the E task (right) for the OCD patients (light gray bars) and comparison subjects (dark gray bars), separately for priming and contingency conditions.

3.3 Event-Related Potentials

ERP results are presented in Figures 6.3 and 6.4. The ANVOA examining N1p amplitudes revealed a significant main effect of task ($F_{1,34}$=23.39; *P*<.001), indicating self-specific suppression of the N1p component. That is, N1p amplitudes were smaller for self-generated effects (ie, in the motor-effect task) than for externally generated effects (ie, in the effect-only task). Furthermore, the effect of task depended upon contingency and, most importantly, the effect differed across groups, as reflected in significant interactions of task x contingency ($F_{1,34}$=9.91; *P*<.01) and task x group ($F_{1,34}$=10.36; *P*<.01). Post-hoc Newman-Keuls tests were performed to further explore these findings. Whereas in control participants the effect of task on N1p amplitudes was highly significant (*P*<.001), patients with OCD showed no self-specific N1 suppression (*P*=.26), as can be seen in Figure 6.4. Moreover, the N1p amplitudes in high as compared to low contingency conditions were found to be suppressed for self-generated effects (*P*=.02), and a tendency for the reverse pattern was present for externally generated effects (*P*=.06).

On the basis of an a priori hypothesis that postulated abnormal motor predictions in patients with OCD, the contingency x task interaction was further parsed with separate follow-up ANOVAs for each group. In the control group, there was a significant interaction of task x contingency ($F_{1,17}$=7.42; *P*=.01), indicating that N1p was modulated by contingency in the motor-effect condition (p=.02) but not in the effect-only condition (*P*=.21), with smaller amplitudes reflecting sensory suppression in high compared to low contingency conditions. In contrast, in patients with OCD, the interaction of task x contingency was not significant ($F_{1,17}$=0.01; *P*=.96), reflecting the fact that N1p amplitudes did not differ between high and low contingency conditions for either self-generated effects (*P*=.60) or externally generated effects (*P*=.64).

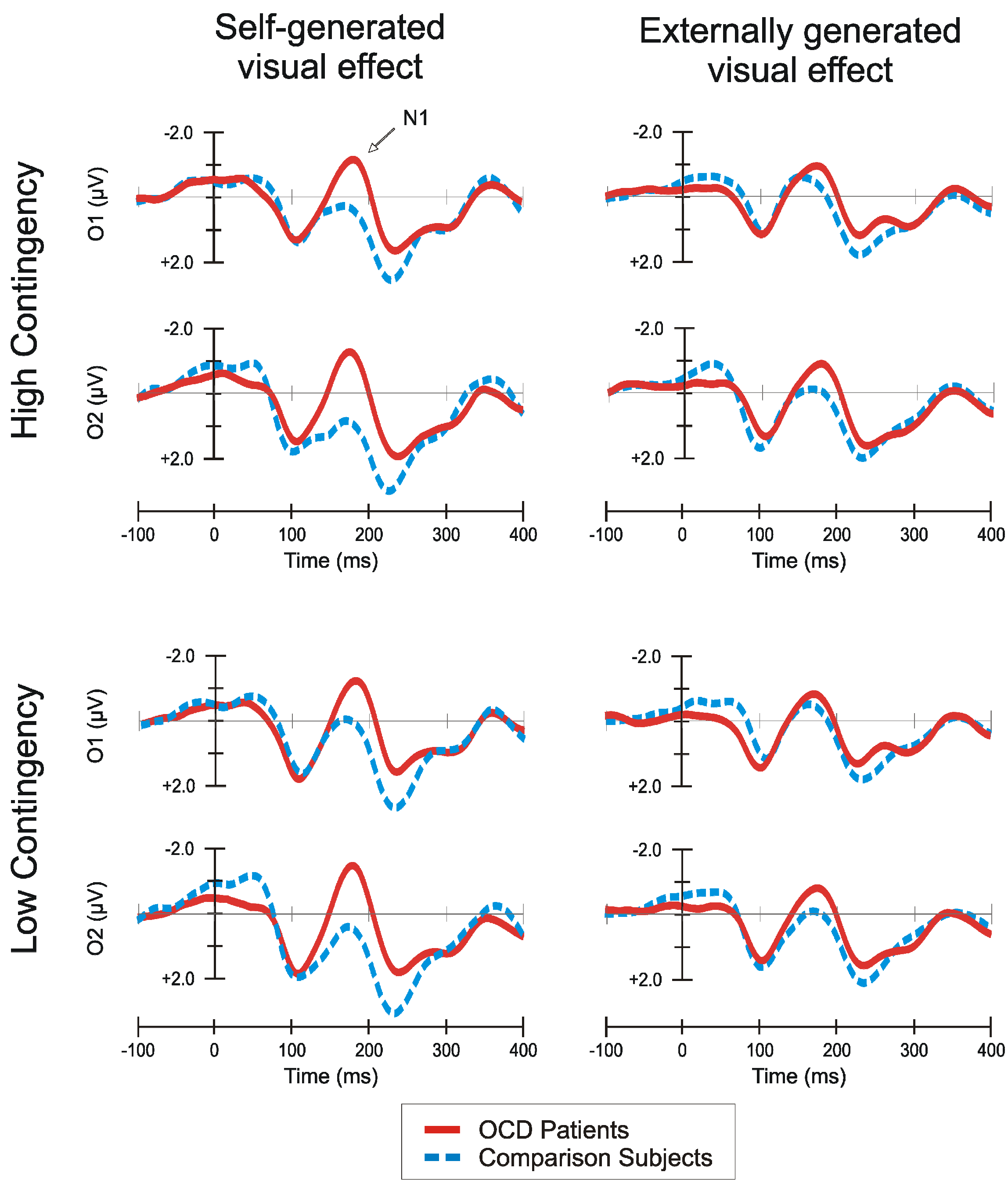

Figure 6.3. Grand average ERPs at electrodes O1 and O2 during active generation of visual effects (left) and passive observation of externally generated visual effects (right), in the two conditions high contingency (upper part) and low contingency (lower part), for healthy comparison subjects (blue) and OCD patients (red).

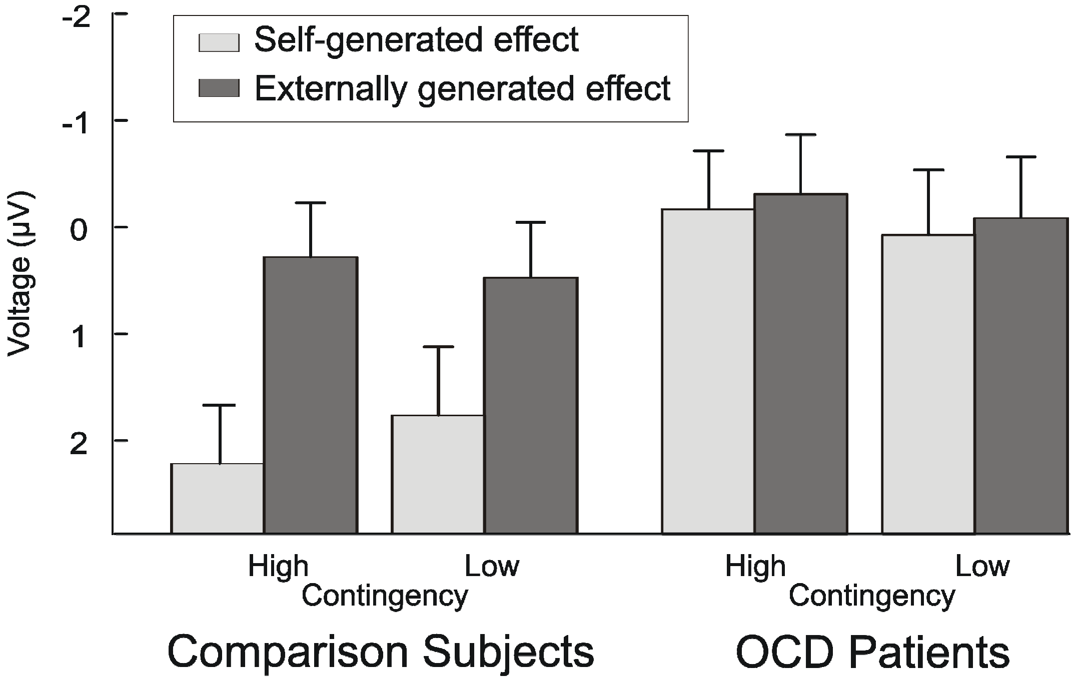

Figure 6.4. Means and standard deviations of the N1 amplitude within the 140-200 ms time window at occipito-parietal electrode sites (O1, O2, PO3, PO4), separately for the ME task (light gray bars) and E task (dark gray bars), contingency conditions (high and low) and groups (OCD patients and controls).

No main effect of group was found ($F_{1,34}$=2.32; *P*=.14). Hence, relative to control participants, patients with OCD had comparable N1p amplitudes. To further explore the possibility of a general hyperexcitability to sensory stimulation the data were analyzed for each task separately. In the motor-effect task, there was a significant effect of group ($F_{1,34}$=4.62; *P*=.04). That is, N1p amplitudes to self-generated effects were significantly smaller in the control group as compared to the patient group, as can be seen in Figure 6.3. During the effect-only task, although it appears that the groups differed in N1 amplitudes, no significant group difference was present ($F_{1,34}$=0.62; *P*=.44). This demonstrates that the group difference in self-specific N1p suppression is due to a specific difference in the processing of sensory stimulation resulting from motor action and not by a general hyperexcitability to sensory stimulation in patients.

No effects involving the factor priming were found at the level of N1p component. Furthermore, the analysis of N1 amplitudes at anterior electrode sites revealed no significant effects involving group or task (all $F<1.98$; all $P>.17$), indicating that N1a amplitudes did not differ between patients and controls nor between self- and externally generated effects.

3.4 Correlations between the Sense of Agency and OCD Characteristics

Pearson correlation analyses and partial correlations controlling for depression (BDI-II) and anxiety (STAI-S) ratings were performed between measures of the sense of agency and clinical characteristics in OCD patients. Positive correlations emerged between mean agency judgments in the ME task and (1) OCI-R "Ordering" score ($r=.74$, $P<.001$; partial $r=.76$, $P=.003$) and (2) OC-TCDQ subtotal for incompleteness ($r=.61$, $P=.007$; partial $r=.54$, $P=.05$). That is, the more OCD Ordering symptoms and sensations of incompleteness a patient had, the higher the agency judgments.

4 Discussion

4.1 Electrocortical Index of Agency

The present study found aberrant sensory gating during processing of action outcomes in patients with OCD. Specifically, instead of showing the suppression of posterior N1 to self-generated visual events that was observed in control participants, individuals with OCD did not distinguish between self and externally generated visual events at these early stages of the information processing flow. Research has revealed that sensory suppression results from forward model predictions of the motor system precisely canceling out the sensory effects induced by action (Blakemore, Frith, & Wolpert, 1999; Blakemore, Wolpert, & Frith, 2000; Sperry, 1950; von Holst & Mittelstaedt, 1950). Within this context of research, the lack of suppression exhibited by patients indicates deficient internal motor predictions, which may explain the tendency of individuals with OCD to continuously register error signals and to experience dissatisfaction in outcome processing (Pitman, 1987; Schwartz, 1997). In line with this interpretation, the present findings further revealed that N1 suppression in control participants was larger when precise motor predictions were available as it were the case in conditions of high action-effect contingency. In contrast, in patients with OCD, N1 amplitudes did not differ between contingent and non-contingent outcomes.

Interestingly, impaired sensory gating in OCD during movement together with enhanced responsiveness to sensory stimuli in OCD patients has been described by a recent study using somatosensory evoked potentials (Rossi et al., 2005). However, due to a general enhancement of cortical activation also in the non-movement condition, the authors argued that cortical hyperexcitability might have caused the inability to modulate sensory input in OCD. Hence, from these findings it remained unclear which role forward model mechanisms may play in deficient inhibitory gating of sensory input in OCD patients. In the present study, in contrast, the difference in N1 amplitudes between patients and controls was specific to conditions involving actions, ruling out unspecific sensory hyperexcitability as a possible explanation. Moreover, the present study not only extends the prior finding by Rossi et al. (2005) by clarifying the mechanism underlying the reduced sensory gating in OCD but also shows for the first time a lack of sensory suppression for distal, not proximal effects in the context of instrumental action. The capacity for instrumental action lies at the heart of agentive self-awareness.

Motor prediction as reflected in sensory gating of action consequences has been shown to rely on an efference copy, a signal generated in cortical areas involved in motor preparation (Voss, Ingram, Haggard, & Wolpert, 2006), such as the supplementary motor area (SMA) (Haggard & Whitford, 2004) and premotor cortex (Berti et al., 2005). The efferent signal is fed into an internal forward model eliciting a perceptual expectation, a so-called corollary discharge, used in cortical and subcortical areas to modulate perceptual processing during action (eg, in somatosensation, Christensen et al., 2007; eg, in vision, Wurtz, McAlonan, Cavanaugh, & Berman, 2011). Hyperactivity of the SMA and premotor areas is a prominent feature in the neurobiology of OCD (Greenberg et al., 2000; Yucel et al., 2007). There is evidence that repetitive transcranial magnetic stimulation to the SMA improves clinical symptoms of OCD patients (Mantovani et al., 2006). Hence, it can be speculated that, in OCD, abnormal cortical activity in the SMA might impair the formation of precise corollary discharge and the fine-tuning of associated sensorimotor integration.

Forward model predictions are utilized by the motor control system for adjusting movements online based on goal achievement, and this is monitored by frontal and posterior control systems (Desmurget & Grafton, 2000; Holroyd & Coles, 2002; Krigolson & Holroyd, 2006). While the posterior error detection system is thought to depend on the integration of sensory inflow and motor predictions, the frontal error detection system compares high-level goal representations and motor predictions. Several lines of evidence implicate dysfunctional performance monitoring in frontomedial regions in the pathophysiology of OCD (Gehring, Himle, & Nisenson, 2000; Riesel, Endrass, Kaufmann, & Kathmann, 2011; Ursu, Stenger, Shear, Jones, & Carter, 2003). Our results extend these findings by suggesting a dysfunction also in the posterior error detection system, which is critically involved in online motor adjustments.

Imprecise sensory predictions in OCD cannot serve the function of canceling and filtering self-produced sensory feedback and in this way may cause a constant mismatch in the comparison between expected and actual sensory outcome of a body movement. These mismatch signals might be related to sensory phenomena in OCD such as feelings of incompleteness and persistent internal error signals even during correctly executed actions. Furthermore, due to impairments in this particular mechanism of motor control, OCD patients should also show deficits in fine-tuned predictive motor adjustments. This prediction might be tested in future investigations recording movement kinematics, for example, during visuomotor conflict, in order to explore the exact link between the observed sensory gating deficits and compulsive behavior in OCD.

4.2 Conscious Agency Judgment

Despite impairments at the sensorimotor level of agency, patients' explicit judgments of agency depended on motor predictions as strongly as those of controls. The finding of increased agency judgments in patients is in line with research suggesting an illusory sense of control in OCD and may reflect a compensation for the distorted feeling of agency (Moulding & Kyrios, 2006; Reuven-Magril, Dar, & Liberman, 2008). Recent cognitive theories of OCD emphasize that the appraisal of experiences in individuals with OCD is characteristically determined and biased by inflated beliefs of special personal responsibility (eg, Rachman, 2002). When considered within this theoretical framework, the observed enhancement of explicit agency judgments in patients may reflect the hyperactivity of a cognitive system evaluating the need for personal engagement during exposure to ambiguous sensory signals associated with actions. Cognitive theories further propose that an important self-perpetuating mechanism in OCD consists of engagement in neutralizing (compulsive) behavior that produces a further increment in perceived responsibility (Rachman, 2002; Salkovskis, 1999). Interestingly, our correlation analyses revealed that the conscious experience of agency increased with the level of incompleteness feelings as assessed with the OC-TCDQ (Summerfeldt, Kloosterman, Parker, Antony, & Swinson, 2001) and with the presence of "Ordering" symptoms as measured with the OCI-R (Foa et al., 2002). Further work is needed to elucidate the interrelation between processes of sensorimotor integration, behavioral adjustment and explicit control beliefs.

Consistent with previous studies, healthy controls benefited from prime-induced expectations (Aarts, Custers, & Wegner, 2005; Sato, 2009), specifically in conditions of high contingency. The lack of prime influence on agency experience in individuals with OCD symptoms is consistent with recent reports (Belayachi & Van der Linden, 2010). It indicates that cue integration at the sensorimotor level and weighting at the judgment level of the sense of agency is different in OCD. It might be speculated that due to "noisy" bottom-up sensorimotor signals and the resulting compensatory increase in agency judgment based on explicit control beliefs, patients are less inclined to rely on additional implicit, sensorimotor based cues.

The typical and most extensively discussed pathology involving a disruption of agency experience are delusions of control in schizophrenia, which have straightforwardly been explained by dysfunctional motor prediction and sensorimotor gating (Frith, 2005; Frith, Blakemore, & Wolpert, 2000). In comparison to this research, our findings, however, confirm the notion that comparator mechanisms based on motor predictions are not sufficient to explain the content of conscious reflections and attributions of agency (Synofzik, Vosgerau, & Newen, 2008a). Our results demonstrate that a disturbed feeling of agency can express itself differentially at higher cognitive levels of agency processing. According to recent views (Synofzik, Vosgerau, & Newen, 2008b), the formation of agency judgments relies on conscious rationalization processes at higher cognitive levels by integrating bottom-up sensory signals and prior beliefs, learning history and context perception. In schizophrenia, the noisy sensory input seems to be integrated into a cognitive system of biased beliefs and delusions (Heinks-Maldonado et al., 2007), whereas in OCD, it may inform a system searching for conscious control (Moulding & Kyrios, 2006) and motivate behavioral strategies for regaining control over external events.

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Appendix A. List of Figures and Tables

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Appendix B. Abbreviations

ANOVA	Analysis of Variance
BDI	Beck Depression Inventory
DSM-IV	Diagnostic and Statistical Manual of Mental Disorders, 4th Edition
EEG	Electroencephalography
EOG	Electrooculography
ERP	Event-Related Potential
ICA	Independent Component Analysis
ISI	Interstimulus Interval
MADRS	Montgomery-Asberg Depression Rating Scale
N1	Negative Component of the ERP around 100 ms Post-Stimulus
OCD	Obsessive-Compulsive Disorder
OCI	Obsessive-Compulsive Inventory
OC-TCDQ	Obsessive-Compulsive Trait Core Dimension Questionnaire
RT	Reaction Time
SCID	Structured Clinical Interview for DSM-IV
SMA	Supplementary Motor Area
SOA	Stimulus Onset Asynchrony
SSRI	Selective Serotonin Reuptake Inhibitor
STAI-S/T	Spielberger State-Trait Anxiety Inventory-State/Trait Form
TMS	Transcranial Magnetic Stimulation
TCA/TeCA	Tri-/Tetracyclic Antidepressant
VAS	Visual Analog Scale
YBOCS	Yale-Brown Obsessive-Compulsive Scale

Erklärung über die selbständige Abfassung der Arbeit

Hiermit erkläre ich, dass die vorliegende Arbeit ohne unzulässige Hilfe und ohne Benutzung anderer als der angegebenen Hilfsmittel angefertigt wurde und dass die aus fremden Quellen direkt oder indirekt übernommenen Gedanken in der Arbeit als solche erkenntlich gemacht worden sind.

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